

A New Account of the Genus *Horsfieldia* (Myristicaceae), Pt 1

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Abstract

The genus *Horsfieldia*, extending from Ceylon to the Solomon Isls. is redefined to exclude the species formerly assigned to *H. macrocoma*. The remaining 100 species are subdivided into 3 sections, viz. (1) the monotypic section *Horsfieldia* with *H. iryaghedhi* from Ceylon, (2) section *Irya* (40 species) and (3) section *Pyrrhosa* (59 species). Section *Irya* contains chiefly species with a 2-valved perianth and is mainly distributed in East Malesia; the species of section *Pyrrhosa* have mainly a 3- or 4- valved perianth and occur in SE. continental Asia and W. Malesia, west of Wallace's Line. A further subdivision of the sections into groups of species of closer affinity is proposed and discussed in the introduction. Warburg (1897) recognized 52 species, Sinclair (1974, 1975) accepted 38 and a number of varieties. The most important characters for the distinction of species are in the male flowers, especially the androecium. Of the presently accepted 100 species, 41 are newly described, and in addition, 14 are new subspecies and varieties. There are 6 new combinations. Most species have rather restricted but well-defined areas of distribution; *H. irya* has a very large range, covering almost that of the genus. The centres of species development are New Guinea and Borneo, and to a lesser extent Malaya-Sumatra.

A survey and discussion of all characters regarded as important in *Horsfieldia* is given. Two kinds of keys are presented: a general key to all species, mainly based on male flowering specimens, and 6 regional keys covering the whole area of the genus, concentrating on vegetative characters, for the identification of female-flowering and fruiting specimens. All 100 species are fully treated and full synonymy, typification, description, notes, and a brief enumeration of distribution and examined specimens are provided. An index of all scientific names pertaining to *Horsfieldia* will be given in Part 3.

Introduction

With the demise of James Sinclair in 1968*, only the general treatment of *Horsfieldia* — the Flora Malesiana precursor of the fourth genus of Malesian Myristicaceae — remained unpublished, but an alphabetical account of the species, which were already all worked out by him, was posthumously printed in *Gard. Bull. Sing.* 27, 1 (1974) 133-141 and 28, 1 (1975) 1-181. Unfortunately a classification system and most keys are lacking in these publications and before the treatment of the family for *Flora Malesiana* could be started, these had to be provided for. Moreover, much recently collected material needed first to be identified and described.

In Sinclair's earlier revision of the family Myristicaceae for Malaya and Singapore (*Gard. Bull. Sing.* 16, 1958) the genus *Horsfieldia* was thoroughly dealt with and keys were supplied. However, in order to grasp the whole genus, which extends over a large area from Ceylon and S. China east to the Solomon Islands and North Australia, I had to scrutinize all the species myself, and this experience led to different ideas about the circumscription of the species as a matter of course.

Because Sinclair had examined an enormous amount of specimens from all major herbaria, I needed only to restrict my study to the Leiden collection complemented by additional, personal visits to BM, K, and P, from where also rather extensive selected material including type-specimens has been put at my disposal as loans to Leiden.

Following a somewhat extended list of criteria, important for species delimitation — among which are the highly diagnostic value provided by the presence of small non-traumatic cork warts on the lower leaf surface, and a more detailed evaluation of the androecium — I was forced to recognize considerably more species than did Sinclair. Apart from new ones, most of the species accepted by Sinclair have been retained in the present study, while others have been redefined, or renamed, or taken out of synonymy, and some taxa accepted by Sinclair subspecifically have been raised in rank. An example of the few abrogated taxa is *H. polyantha* Warb., also accepted by Sinclair but presently reduced to *H. laevigata*, a name which was reduced by Sinclair to *H. parviflora*.

In Sinclair's enumeration of all species in his 1974/1975 publications, species descriptions of the wide-spread *H. irya* as well as that of the variable and deviating *H. macrocoma* are lacking. The latter possibly has some indicative value as, during the present study, it has appeared that some species to be recognized within the *H. macrocoma*-complex could be better segregated into a new genus, *Endocomia*.

Where my circumscriptions of species differ from Sinclair's, brief reasons are given in the notes.

The Characters in *Horsfieldia*

When Sinclair (1958) dealt with *Horsfieldia* for Malaya, he provided a rather limited discussion of useful species characters, and in his posthumous publication on the genus as a whole (1974, 1975), an explanation of the underlying considerations

* Obituary in *Gard. Bull. Sing.* 23 (1968), pp. i-xxiv.

for the delimitation of the species is only given in the notes to the alphabetically arranged descriptions of the species. In those treatments of the Malayan species, two keys to all species were presented, one for fertile (male flowering) specimens, and one for sterile material and fruit. From these keys it can be learned that he regarded the following characters as important for the distinction of the species: (1) perianth either 2- or 3-valved and (2) shape of the androecium (longer than broad or the reverse, with or without a depression at the top); apparently of lesser importance to him were (3) lenticels on twigs, distinct or not, (4) size of the male perianth and length of the pedicel, (5) some properties of the leaves such as size and texture of the blade, whether glabrous or pubescent beneath, and above, nerves either raised or sunk; and, a further number of specific characters used for the distinction of some individual species.

Although Warburg (1897), Sinclair and I use essentially the same characters for the generic division, I agree with Sinclair (1958, p. 370) in discarding Warburg's subdivision into three sections; Sinclair had advocated a more natural division into two sections i.e., on the basis of how most of the perianths in a specimen split at anthesis, in 2 or 3 valves. I also have the feeling that this criterion is one of the most important characters for a generic division, one that has phylogenetic significance. However, in the case of *H. iryaghedhi* from Ceylon, I have set that apart because it deviates from all the other *Horsfieldias* in various ways.

Characters, which in my opinion, are important for distinguishing groups of species are given further on. They are also used in the list of species with a provisional indication of grouping closer allied species, as presented and discussed in the next chapter on the subdivision of the genus. Special attention is given to the vegetative characters because the genus is dioecious and hence in much of the material the most important taxonomical characters of the male flowers are lacking.

Measurements given in the descriptions of the species and used in the keys based on vegetative characters and fruits are all taken from dried material; those of flowers have all been measured after softening by boiling.

Vegetative characters

(1) *Habit*

The size of the tree sometimes seems specific, but most species are of medium size. *H. sylvestris* with a recorded stature of up to 60 m high ranges among the tallest whereas *H. crux-melitensis* is a shrub or shrubby treelet of 2-4 m. The growth of the main stem is essentially orthotropic with the phyllotaxis dispersed, while the plagiotropic side-branches are generally \pm horizontal or drooping, with the phyllotaxis distichous. Characters of bark, buttresses, stilt roots etc., are mainly observations of Sinclair, as he was acquainted with the species in the field.

(2) *Indumentum*

As in *Knema*, the indumentum of the leaf bud, leaves and twigs, and of the inflorescences and flowers has proved to be important for the delimitation of the species (de Wilde, 1979, p. 324). Except for the flowers of some species, all the above-mentioned parts of the plant are initially covered by a tomentum, but this may be shed at a very early stage. Although there may be minor differences, generally within the same specimen, the nature and size of the tomentum-hairs on the various parts are largely similar, and to a large degree characteristic of the taxa. For practical reasons, the tomentum is described only in a general way, the lengths of the hairs (which themselves may be very complex) appearing to be of considerable importance for the recognition of the species. Much on the tomentum can be found in the study on the comparative leaf anatomy of the Asiatic Myristicaceae by Koster and Baas (1981).

(3) *Twigs*

The indumentum of the twigs is generally shed very early but sometimes may remain on the young innovations; it is generally similar to that of the leaf bud and can be simultaneously judged if required for the determination with the keys. The internodes in the leaf-bearing portion may be terete or faintly lined. Sometimes these lines, which run from both sides of the insertion of one petiole to the next, are very pronounced and may render the twig angular or faintly winged, which is characteristic for several species e.g., *H. brachiata*. The bark of older twigs i.e., behind the leaves and often where the infructescences are inserted, may be striate to various degrees; only in rare cases does older bark flake more or less characteristically or crack longitudinally, as in *H. sabulosa*, *H. xanthina* or *H. disticha*. The bark of young twigs usually dries brown or dark brown, contrasting little with the dark colour of the dried petioles, but in some species (e.g., *H. spicata*, *H. oligocarpa*, *H. pallidicaula*), the twigs dry to a conspicuously pale, greyish or straw-colour, contrasting well with the petioles, and the discrepancy is then used in the keys. Slightly older bark nearly always bears lenticels, rather characteristically small or large, often paler and contrasting well with the twig but at other times merging in colour and then inconspicuous. In passing, it should be noted that the presence of lenticels in Malesian taxa of the family seems to be largely or wholly restricted to the genus *Horsfieldia*.

In the descriptions, the diameter of twigs was measured not far below the apex in the leaf-bearing portion while the size cited in parentheses was taken lower down where old inflorescences or infructescences may be attached. Excepting *H. sabulosa*, *Horsfieldias* never flower on the older wood.

According to Armstrong and Wilson (1980) the wood of *Horsfieldia* is very homogeneous and of little taxonomic value at a specific level. At the generic level, it can be distinguished from the other three Asiatic genera of Myristicaceae. The wood of one specimen of *H. macrocoma* (placed in a new genus *Endocomia* de Wilde, 1984) is apparently not significantly distinct from wood of other *Horsfieldias*.

(4) *Phyllotaxis*

In the majority of the species, leaves of the plagiotropic twigs i.e., generally the fertile ones, are distichous. In some species, phyllotaxis is characteristically dispersed, mostly with leaves in 3-5 rows (e.g., *H. kingii*, *H. thorelii*, *H. sucosa*, *H. sabulosa*); only in a few species are the leaves either distichous or dispersed and sometimes phyllotaxis is mixed as in one collection. The phyllotaxis is usually very obvious and easy to see in older twig-portions, hence it is used in the keys. Those species which have a variable phyllotaxis have been entered in the keys twice.

(5) *Leaves*

As a matter of course, many features of the leaves, as shape, size, texture, drying colour, number of lateral nerves and length of the petiole are of importance for the recognition of the species, but only some characters of special interest will be briefly discussed here (a-e).

(a) *Pale markings on the upper surface*

Often present in many species are very small markings, regularly spaced and usually slightly raised. Their origin is unknown to me. In a few species, much larger, pale-coloured, often nearly white blotches of irregular shape and unpredictable location may prevail, sometimes only in a part of the leaves or only locally present on some of the leaves. They are likely to be an artifact of drying, of unknown origin and may be found in e.g., *H. smithii*, yet they are very characteristic of almost all *H. irya* collections.

(b) *Blackish or brown markings on the lower leaf-surface*

A fine, pale, or more often a dark punctation in the form of small blackish dots, possibly tannic conglomerations, is often present in many species, also in

the fleshy tissue of perianths, androphores, or pericarps. Furthermore, there is in certain species a very specific coarser punctation, regularly spaced dots of c. 0.1 mm diam., being a sort of non-traumatic cork warts of unknown origin, most likely originating from hair-bases or hair scars. The presence or absence of these dots should always be checked when determining a specimen, their presence being very distinctive for several species e.g, *H. punctatifolia*, *H. glabra*.

(c) *Nerves*

In most species, whether midrib and nerves above are flattish, sunken, or distinctly raised, is of diagnostic significance. For the identification of a few "difficult" species as e.g., the distinction between *H. whitmorei* and *H. laevigata*, it is important to check on the submarginal nerve i.e., whether its arches are particularly marked and regularly shaped as is the case with the former species against the less distinctive and less regular in the latter.

(d) *The terminal leaf bud*

The terminal leaf bud is usually present in every collection. It shows up as a long subterete or \pm flattened cone, usually at least five times longer than broad; in some species however, mainly in those with the leaves dispersed, it is shorter and broader. The tomentum of the leaf bud, especially the length of the hairs, has proved to be a good diagnostic character, as also indicated under item 2.

(e) *Petiole*

The petiole is usually well-developed. *H. sessilifolia* and much material of *H. sylvestris* have almost sessile leaves; the petioles of *H. sabulosa* are the longest in the genus, up to 5 cm long.

Generative characters

(6) *Inflorescences*

The inflorescences are generally situated on the younger twigs, in-between the older leaves or not far behind. Only in *H. sabulosa* does flowering occur on older wood. They are almost always panicle-like (spike-like in most of *H. spicata*), (2 or) 3 or 4 times ramified, the mode of branching being essentially racemose. Flowers are borne on the ultimate branches, either solitary or grouped in loose clusters of up to 10 each in the male inflorescence; those of *H. sylvestris*, especially in young inflorescences, may be clustered in rather dense heads, but in the rather deviating species *H. iryaghedhi*, the male flowers are grouped in true dense heads each with up to nearly one hundred flowers.

In general, all flowers of an inflorescence of both sexes are of about the same age or stage of development, only in *H. amygdalina* is there a tendency of some to develop ahead of the others. This latter situation is prevalent in the segregated genus *Endocomia* which contains the species *E. macrocoma* formerly placed in *Horsfieldia*.

Branching is subtended by bracts except the one bearing the ultimate flowers, the bracts falling off early in all cases. Bracteoles are absent in *Horsfieldia*, the segregated genus *Endocomia*, and *Gymnacranthera* but present in *Knema* and *Myristica*.

At the base of the inflorescence there are always a few cataphylls, short and triangular in outline and clothed with a tomentum similar to that on the inflorescences, leaf buds and twig-apices.

The largest inflorescences, to c. 30 cm long, are found in *H. ampla* and *H. ampliformis* from New Guinea. In almost all species the male inflorescences are larger and more elaborate as compared with the female ones; only in *H. parviflora* are male and female inflorescences often equal in these respects.

Following flowering, at fruiting stage, whole inflorescences are discarded as in *Endocomia*, *Gymnacranthera* and in some *Myristica*, hence unlike the situation in *Knema* and the rest of *Myristica* where flowering occurs on woody brachyoblasts, or short shoots which are essentially of unlimited growth.

(7) *Flowers*

The flowers are unisexual, dioecious. The perianth of the male is usually smaller than that of female flowers (considerably so in e.g., *H. thorelii*), or they are equal, or even considerably larger in size. Their size is fairly constant for each species. For instance, in *H. parviflora* which was described from a female specimen, the perianth of the female flower is considerably smaller than the male perianth which is one of the largest found in *Horsfieldia*, up to 4 mm wide.

According to the species, the perianth may be cleft into predominantly 2 or 3 (or 4) valves, and it is on this character that the division of the genus into sections is based. It is of interest to mention here that this manner of sectional division coincides well with the various distributional areas as is pointed out in the next chapter, on distribution.

The extent of the split of the perianth at anthesis varies with the species and cleaving outright or almost to the base (in male flowers) is limited to only a few species. At anthesis, the perianth opens only a little, the lobes neither horizontally spread nor curved nor reflexed as is often the case in *Knema*, *Myristica*, *Gymnacranthera* and always in *Endocomia*.

The flower colour ranges from yellowish green to a bright yellow or orange-yellow.

The consistency of the perianths may be diagnostic for the species, especially of male specimens, and sometimes it is useful to note whether the perianth collapses on drying or not. Flowers may be glabrous, or very early glabrescent; or they are pubescent, sometimes only so toward the perianth base or the pedicel. The inner surface of the perianth is always glabrous, in contrast with species of *Endocomia*, formerly included in *Horsfieldia* as *H. macrocoma* s.l.; it is only in *H. subtilis* var. *rostrata* (formerly *H. rostrata*) that the inner side of the female perianth was originally described as pilose, but I have not seen that specimen.

(8) *Staminate flowers*

Staminate flowers provide for the taxonomically most important characters, at various levels.

(a) The shape of the *male perianth* shows much variation. In the 2-valved species, the perianth is generally laterally compressed, in outline either circular, or pear-shaped, or reniform, but in *H. irya* which is the type of the 2-valved section *Irya*, it is subglobose and not or but little compressed. The perianth of the 3- or 4-valved species, prevalent in sect. *Pyrrhosa*, is usually globose or pear-shaped and not laterally compressed but sometimes apically depressed, and of various sizes. *H. crassifolia* has a 2-valved but globose perianth, and also because of its non-compressed androecium, joins taxonomically the 3-valved species in sect. *Pyrrhosa*.

Peculiarly long-conical 2-valved male flowers prevail in *H. crux-melitensis*, *H. clavata*, and *H. squamulosa*; they have club-shaped androecia, aberrant for the genus, as discussed below.

(b) The *depth to which the perianth is cleft* at anthesis is a diagnostic character for several species. Sometimes the perianth opens only at the very top e.g., in *H. triandra*, *H. crux-melitensis*, *H. sterilis* and *H. pulverulenta*; in others it is split to the base or nearly so e.g., in *H. basifissa*, *H. angularis*, *H. obscura* and several others, but in most species it is split to about halfway.

(c) The *pedicels* are usually cylindrical or subterete, sometimes subtriangular (in species of the group *H. polyspherula*), slender or thickish, and it may be of taxonomical importance whether they are longer or shorter than the perianth. In some species with pear-shaped or club-shaped flowers e.g., *H. tuberculata* (partly so), or *H. crux-melitensis*, *H. lancifolia*, *H. decalvata* and some others, the base of the perianth gradually narrows into a tapering pedicel.

In many species the pedicel is typically articulated at the base, at least in dried specimens; however, in a few species including *H. glabra* this character does not seem to be very constant. One should be aware that the bracteal scars of the uppermost inflorescence may be mistaken for the articulation in the pedicel and therefore several pedicels should be checked. Bracteoles are lacking in *Horsfieldia*, as already noted.

(d) The *androecium* of the male flowers shows much diversity in shape and construction and provides the most important characters in the delimitation of species. Again, at the generic level, the androecium also provides major characters.

In *Horsfieldia*, as in the other Asiatic Myristicaceae, the stamens are always connate through presumably the fusion of filaments into an androphore, which usually bears a so-called central column. The androphore is generally rather short and may be absent. The degree of coalescence of the anther-bearing part or synandrium varies according to the species; in many, the anthers are completely connate or almost so, at their back, forming a broad central column usually of a rather spongy texture and showing much specific variation in shape. In many other species the coalescence of the anthers is only partial and the anthers may then have free apices of various lengths, depending on the species. Opening of the thecae is extrorse to *latror-* (directed sideways).

A well-developed central column, if present, may be solid, but in the majority of the species it is hollowed out in the apical portion in very diverse ways and to various depths, according to the species. The anthers may be erect or suberect, or curved and following the straight or rounded shape of the central column. The free portions of the anthers, if prevalent, may stand erect or curve inwards into the central-apical cavity of the central column to various depths according to the species. The androecium may be elliptic in transverse section, as in most species with a laterally compressed 2-valved perianth (sect. *Irya*); or circular or subcircular as in most species with 3 or 4-valved perianths (sections *Iryaghedhi* and *Pyrrhosa*). In the group of *H. polyspherula* (sect. *Pyrrhosa*) the anthers are typically erect or suberect, mutually free for the upper half while the androecium is typically triangular in transverse section.

Each anther consists essentially of a pair of bisporangiate lobes or thecae, comparable to those of the presumably more primitive condition found in *Compsonaura* and *Dialyanthera* (S. America), or *Brochoneura* (Africa) where the anthers are monadelphous with their filaments fused only towards the base. Armstrong and Wilson (1978, fig. 16) postulate that there is within *Horsfieldia* an evolutionary trend in the androecia from a condition of a relatively poorly developed central column, or a small degree of fusion of the connective columns and hence with more protrusion of the anthers, towards one with a greater fusion in the connective column (i.e., a broad and well-developed central column) and a reduction in the protrusion and pairing of the anthers. The least specialized conditions i.e., with relatively free anthers, would be those as found in species like *H. irya*, *H. parviflora*, or *H. ardisiifolia*, all with a predominantly 2-valved perianth i.e., in sect. *Irya*.

Schematic longitudinal and transverse sections of the typical androecium forms of almost all species are represented in figure 1A-D. I have refrained

from hypothesising as regards which forms may be more primitive or more advanced, though in general, I agree with Armstrong and Wilson.

The number of anthers is generally a good species character, although in some cases, it may vary considerably. When the anthers are tightly set, they may be difficult to count, especially because they are much elongated and consist of two equal thecae.

The size of the androecium in relation to the perianth is sometimes significant; usually it almost completely fills the perianth, but in e.g., *H. amplifloris*, the perianth is largely hollow because the androecium occupies only a fraction of the space.

It is peculiar that in juvenile stages the thecae of the anthers may be typically septate, the septa being of non-tapetal origin; this phenomenon has been studied by Armstrong and Wilson (1978). I am not sure whether it occurs in all species of *Horsfieldia*. Such a septation is unknown in *Myristica* and *Knema*.

(9) *Pistillate flowers*

The female perianth is usually subglobose, ellipsoid or ovoid, and the shape varies somewhat with the species. In most species the female flowers are larger than the male for example, distinctly so in *H. thorelii*, but many exceptions exist. Within the same species the number of perianth-valves is always similar in male and female flowers, but the extent of the split in female flowers is usually considerably less.

The globose, ellipsoid or ovoid ovary may be glabrous or hairy, according to the species. There is some variation in the size and shape of the stigma, which is essentially 2-lipped and the style is usually absent or very short. In general, the small differences in the stigma are difficult to describe and this has not been exhaustively studied by me. *H. squamulosa*, for instance, has a relatively long, erect, slender style and stigma, which show up as a minute appendage on the young fruit; in *H. sepikensis* the stigma is sessile and conspicuously broad-lipped; in *H. iryagedhi* the sessile stigma tends to be few-lobulate and not 2-lobed.

(10) *Fruits*

The fruit agrees in general appearance with other myristicaceous fruit, but is in *Horsfieldia* (and in the genus *Knema*) characterized by the aril being either complete or split into short laciniae in the apical portion only. The pericarp is glabrous or pubescent; in the latter case the hairs may remain only at the very base of the fruit, near the insertion of its stalk. Fruit size is largely diagnostic for the species. The fruit of *H. grandis*, c. 1 cm long, is among the smallest, that of *H. punctatifolia*, up to 8 cm long, is among the largest in the genus. In variable species like *H. polyspherula* and *H. pallidicaula*, I have accepted several varieties mainly on the basis of fruit size. The shape of the fruits is usually short-ellipsoid, and of the seed, ellipsoid; only in a few species is the fruit globose or nearly so e.g., in *H. subtilis* var. *subtilis* and *H. sinclairii*, but their seeds are short-ellipsoid; in *H. irya* fruit and seed are globose.

The pericarp varies in thickness according to the species; it is hard-succulent in the fresh state, shrinking considerably on drying. For example, the pericarp of large fruits of *H. punctatifolia* would usually shrink from a 4-cm thickness when fresh to 1 cm. The surface of the dry pericarp is in many species provided with conspicuous pale warts or dots, apparently becoming more pronounced with drying, showing up as lenticel-like tubercles. A striking example is the fruit of *H. laevigata*.

Finally, it may be remarked here that in several species the female perianth remains persistent under the fruit. This phenomenon occurs in species which are, if considered on other grounds, not regarded as closely related. However, it provides an easily observed character for species like *H. kingii*, *H. wallichii*, *H. splendida*, *H. pallidicaula* and others.

Description and Redefinition of the Genus *Horsfieldia**Horsfieldia* Willd.

Horsfieldia Willd., Sp. Pl. 4 (1806) 872 [non Bl. = *Harmsiopanax* Warb. (Aral.)]; Pers., Symb. 2 (1807) 635; Warb., Mon. Myrist. (1897) 130, 262; Sinclair, Gard. Bull. Sing. 16 (1958) 368; 27 (1974) 133-141; 28 (1975) 1-181. — *Pyrhosa* Endl., Gen. Pl. (1839) 830 (see note). — Type: *Horsfieldia odorata* Willd. = *H. iryaghedhi* (Gaertn.) Warb.

Myristica sect. *Pyrhosa* Bl., Rumphia 1 (1837) 190-192, Tab. 62-64. — With subsequent authors the genus *Horsfieldia* as presently defined was treated partly under *Myristica* sect. *Pyrhosa* as well as under several other sections of *Myristica* viz., sects. *Caloneura* p.p., *Eumyristica* p.p., *Horsfieldia*, *Irya*; see Sinclair (1958), p. 368 and under the presently accepted sections. — Lectotype of *Myristica* sect. *Pyrhosa*: *Myristica glabra* Bl. = *Horsfieldia glabra* (Bl.) Warb.

Shrubs or usually trees, 2-40 (-60) m, dioecious. Twigs usually early glabrescent, terete or sometimes angular or with two raised lines or ridges from petiole to petiole, bark usually striate, always lenticellate but sometimes inconspicuously so. Leaves distichous or in some species dispersed, usually petioled, blades up to 45 cm long, membranous to coriaceous, often brittle when dry, pubescent or glabrescent, nerves prominent or not above, reticulations above usually lax, never forming a dense, close network as in *Knema*, lower surface not glaucous, papillose (alveolar tissue) only in *H. iryaghedhi*; in some species non-traumatic cork warts present. Inflorescences axillary, situated in between and behind the leaves, rarely on the older wood (*H. sabulosa*), paniculate, usually branched several times, pubescent or glabrescent, at base of common peduncle with a few minute cataphylls; female inflorescences usually smaller than the male. Flowers usually pedicelled, glabrous or pubescent, solitary or in loose, sometimes sub-umbellate clusters or fascicles, generally all of about the same age in the same inflorescence, in *H. iryaghedhi* the male with flowers sessile in dense flower-heads; bracts broad-triangular to elliptic or boat-shaped, caducous. Perianth thin-leathery to succulent, either 2 (or 3) or (2 or) 3- or 4-lobed, inside glabrous, greenish to yellowish, never red, the lobes splitting the perianth to various depths, never spreading; bracteoles absent. Male perianth usually small, either globose, depressed-globose, transversely ellipsoid, ellipsoid, reniform, pear-shaped, or clavate, laterally compressed or not. Androecium very diverse in shape, either cupshaped, or globose to ellipsoid, cylindrical, or trigonous, laterally compressed or not, sessile or with short androphore; the anthers usually entirely or largely mutually connate and adnate at their back into a narrow or broad central column various in shape, the latter usually with a depression or excavation to various depths at apex. Anthers 2-c. 25, either straight and \pm erect, or curved or the apical parts incurved or inflexed into the cavity of the column to various depths; thecae often septate in the juvenile stage, opening extrorsely. Female perianth usually larger than the male, subglobose to ovoid-ellipsoid; ovary globose or ovoid, glabrous or pubescent, style absent, stigma 2-lobed or 2-lipped, usually small, more-lobed only in *H. iryaghedhi*. Infructescences of moderate size, smaller than male inflorescences. Fruits globose or usually ellipsoid, pericarp usually somewhat fleshy, drying brown or blackish, often with lenticel-like tubercles, glabrous or pubescent, or subglabrescent, perianth sometimes persistent under the fruit; seed ellipsoid, rarely globose, testa not variegated; aril completely covering the seed, entire or at apex shallowly lobed or convoluted; albumen ruminant, with fatty oil but no starch; cotyledons connate at base.

NOTES

Fieldnotes. Trees of primary rain forest, often persisting in secondary growth; also in marshy forest, and stilt roots present in some species.

According to Sinclair (1958) the bark of Malayan species is usually reddish-brown, smooth or more often striate or rough with circular or irregular dents, sometimes flaking but mostly not. The flowers are mostly waxy yellow, and often sweet scented; those of *H. iryaghedhi* have a particularly strong smell.

Anatomy. Koster and Baas (1981) published a paper on the comparative leaf anatomy of the Asiatic Myristicaceae and found the genera anatomically quite distinct, especially in the hairs and the vascular pattern of the midrib and petiole; most species examined can be distinguished by their epidermal features.

Taxonomy. After having examined all species of *Horsfieldia*, including *H. macrocoma*, I came to the conclusion that within *H. macrocoma* s.l. four species could be distinguished. These rather deviate from all other *Horsfieldias* and I have segregated them into a new genus *Endocomia* (1984), which differs from *Horsfieldia* by the following characters: flowers monoecious; flowers at the ultimate ramifications of the inflorescences developing in rather different stages; perianth inside hairy or with appendages, at anthesis cleft to the base into (3 or) 4 (or 5) valves and these spreading or recurved and not erect; androecium long-stalked, of different construction; aril generally lacinated to about halfway the seed or more; testa of the seed variegated.

Synonymy. *Pyrrhosa* Endl. is illegitimate because *Horsfieldia* Willd., as genus, is cited in its synonymy; according to art. 7, 11 of the Code, *Pyrrhosa* Endl. should be typified by *Horsfieldia odorata* Willd., being the type of the name which should have been adopted. *Pyrrhosa* Bl. as section is presently lectotypified by *Myristica glabra*, a practice initiated by Hook. f. and Thomson (1855) with the division of *Myristica* sect. *Pyrrhosa* Bl. into three sections of smaller circumscription viz., sect. *Eumyristica*, sect. *Irya*, and sect. *Pyrrhosa*; these three coincide largely with the three presently accepted sections in *Horsfieldia*.

Table I

Table I enumerates all species in *Horsfieldia* and indicates by horizontal lines demarcations between accepted sections and informal groups of species; broken lines indicate marked discrepancies within a group as is discussed in the text.

The distribution of three marked characters which are used at species level, but not primarily used to distinguish sections or groups, is indicated with symbols before the species names. A deviating perianth valve-number within a section is indicated between the brackets; □ = pedicel articulated at base, + = perianth persistent under the fruit, • = lower leaf surface with coarse dark-coloured dots from cork warts.

+		1. <i>H. iryagedhii</i>			17. <i>H. olens</i> (valves 3)
		2. <i>H. kingii</i> (valves 4)			18. <i>H. sepikensis</i> (valves 3)
		3. <i>H. longiflora</i> (valves 2)			19. <i>H. sylvestris</i>
		4. <i>H. thorelii</i> (valves 2 or 3)			20. <i>H. australiana</i>
		5. <i>H. amygdalina</i> (valves 2 or 3)			21. <i>H. crux-melitensis</i>
		6. <i>H. irya</i>			22. <i>H. clavata</i>
		7. <i>H. spicata</i>			23. <i>H. squamulosa</i>
	•	8. <i>H. inflexa</i>			24. <i>H. ampla</i>
		9. <i>H. moluccana</i>			25. <i>H. ampliformis</i>
		10. <i>H. parviflora</i>			26. <i>H. angularis</i> (valves 2-4)
		11. <i>H. obscurinervia</i>			27. <i>H. iriana</i>
		12. <i>H. ardisiifolia</i>			28. <i>H. aruana</i>
		13. <i>H. talaudensis</i>			29. <i>H. subtilis</i>
		14. <i>H. samarensis</i>			30. <i>H. schlechteri</i>
		15. <i>H. smithii</i>			31. <i>H. basifissa</i>
		16. <i>H. palauensis</i>			

			32. <i>H. sinclairii</i>	+	<input type="checkbox"/>	66. <i>H. affinis</i>
			33. <i>H. psilantha</i>		<input type="checkbox"/>	67. <i>H. reticulata</i>
			34. <i>H. whitmorei</i>	+		• 68. <i>H. crassifolia</i> (valves 2)
			35. <i>H. laevigata</i>			69. <i>H. carnosa</i>
			36. <i>H. pilifera</i>	+		70. <i>H. sterilis</i> (valves 2)
			37. <i>H. lancifolia</i>		<input type="checkbox"/>	71. <i>H. hirtiflora</i>
			38. <i>H. decalvata</i>		<input type="checkbox"/>	72. <i>H. brachiata</i>
			39. <i>H. tuberculata</i>		<input type="checkbox"/>	73. <i>H. pachyrachis</i>
			40. <i>H. corrugata</i>		<input type="checkbox"/>	74. <i>H. ridleyana</i>
			41. <i>H. pachycarpa</i>		<input type="checkbox"/>	75. <i>H. obtusa</i>
			42. <i>H. pulverulenta</i>		(<input type="checkbox"/>)	76. <i>H. disticha</i>
			43. <i>H. leptantha</i>		(<input type="checkbox"/>)	77. <i>H. tenuifolia</i>
			44. <i>H. hellwigii</i>		<input type="checkbox"/>	78. <i>H. macilentia</i>
			45. <i>H. ralunensis</i>		<input type="checkbox"/>	79. <i>H. laticostata</i>
	<input type="checkbox"/>	•	46. <i>H. sabulosa</i>		<input type="checkbox"/>	80. <i>H. nervosa</i>
(+)	<input type="checkbox"/>	•	47. <i>H. atjehensis</i>		<input type="checkbox"/>	81. <i>H. polyspherula</i>
(+)			48. <i>H. sucosa</i>		<input type="checkbox"/>	82. <i>H. oligocarpa</i>
			49. <i>H. pallidicaula</i>			83. <i>H. endertii</i>
			50. <i>H. sparsa</i>	(+)		84. <i>H. valida</i>
			51. <i>H. triandra</i>		<input type="checkbox"/>	• 85. <i>H. borneensis</i>
			52. <i>H. tristis</i>	+		86. <i>H. fragillina</i>
+	(<input type="checkbox"/>)		53. <i>H. fulva</i>	+		87. <i>H. androphora</i>
+			54. <i>H. superba</i>		(<input type="checkbox"/>)	88. <i>H. amplomontana</i>
			55. <i>H. sessilifolia</i>			89. <i>H. montana</i>
			56. <i>H. grandis</i>			• 90. <i>H. punctata</i>
+		•	57. <i>H. wallichii</i>			91. <i>H. costulata</i>
		•	58. <i>H. pulcherrima</i>			92. <i>H. subalpina</i>
+			59. <i>H. flocculosa</i>			93. <i>H. obscura</i>
			60. <i>H. motleyi</i>		<input type="checkbox"/>	94. <i>H. xanthina</i>
			61. <i>H. tomentosa</i>			95. <i>H. majuscula</i>
+			62. <i>H. gracilis</i>			96. <i>H. coriacea</i>
			63. <i>H. paucinervis</i>			• 97. <i>H. penangiana</i>
+			64. <i>H. splendida</i>			• 98. <i>H. punctatifolia</i>
	(<input type="checkbox"/>)		65. <i>H. rufo-lanata</i>		(<input type="checkbox"/>)	• 99. <i>H. macrothyrsa</i>
						• 100. <i>H. glabra</i>

Subdivision of *Horsfieldia* into Three Sections

As can be seen in the preceding survey of characters to be used in the taxonomy of *Horsfieldia* as well as from the species descriptions, there is a large diversity in the genus. This led Warburg (1897) to subdivide the genus into 3 sections, with 5 subsections and 2 series, with 11 additional accepted species not placed in any section because their male flowers were unknown. Warburg's subdivision appears to me very artificial, at least for the greater part. For the Malayan species only, Sinclair (1958) advocated a more simple subdivision into "Bivalves" and "Trivalves", and some unnamed subsections, but a definite decision, pending on the study of the whole genus, was frustrated by his early death.

I have chosen to subdivide the 100 presently accepted species into three sections although I realize that these are of considerably unequal taxonomic weight. The three are: (1) sect. *Horsfieldia*, containing one single species, being the type species of the genus, but rather deviating from all others, (2) sect. *Irya*, containing most species with a predominantly 2-valved perianth, and (3) sect. *Pyrrhosa* with most species having predominantly a 3- or 4-valved perianth. Although the two last-named sections, which are by no means sharply segregated but which have their own range of distribution, coincide with Sinclair's subdivision, they should be named differently on nomenclatural grounds. Each contains a few species with the perianth predominantly of a deviating valve-number, but it will be argued in the discussion on the groups that these species are tentatively best regarded as casual deviations still to be placed in that section.

As regards a further formal subdivision, I have refrained from making any. Instead, I have listed in Table I all the species and indicated with horizontal lines (either continuous, or broken, according to the supposed strength of the demarcations) which groups or clusters can be distinguished. These groups, without formal status, contain species which are presumably closer to each other on grounds to be discussed in the next chapter. At first sight several of these groups of more or less coherent species seem to represent formal entities e.g., subsections or series, but in view of the diversity in the variation of all species concerned, this certainly would lead to a complicated system of entities differing much in taxonomic weight and with blurred circumscriptions.

It is obvious that the species in general have reticulate relationships, and the groups are only consistent on the basis of a single or a few putatively important characters. Other characters, which could be regarded as important as well will often be found distributed in various other groups, without necessarily expressing that such characters, respective to their groups, are less valuable or the groups unnatural. The erratic distribution of such characters not used to assemble species into groups, as the presence of non-traumatic cork warts on the lower leaf surface, the presence of an articulation at the base of the pedicel, or the calyx being persistent under the fruit, is indicated in the list of species in Table I, according to the symbols explained in the legend. I have refrained from arguing about any phylogenetic value of these groups as I feel that it is arbitrary and difficult to judge what characters should rank phylogenetically behind others, and often, one can only guess which character-states should be ranked as more primitive or more advanced.

The sections and groups will be discussed briefly below, with references to links with other groups or individual species. The majority of the characters binding a group can be extracted from those used subsequently in the general key to the species.

The Sections and a Survey of the Groups

1. Sect. *Horsfieldia*

Myristica sect. *Horsfieldia* A. DC., Prod. 14 (1856) 200; Miq., Fl. Ned. Ind. 1, 2 (1859) 63. — *Myristica* sect. *Irya* auct. non Hook. f. & Th.: Benth. & Hook.f., Gen. Pl. 3 (1880) 137, for *Horsfieldia* Willd. only. — *Myristica* sect. *Eumyristica* subsect. *Horsfieldia* (A. DC.) King, Ann. Roy. Bot. Gard. Calc. 3 (1891) 282. — Type: *Horsfieldia odorata* Willd.

Myristica sect. *Pyrrhosa* Bl., Rumphia 1 (1835) 190, p.p., for *M. horsfieldii* only, not the lectotype. — *Myristica* sect. *Eumyristica* Hook.f. & Thomson, Fl. Ind. (1855) 162, p.p., for *M. horsfieldii* only.

Horsfieldia sect. *Orphanthera* Warb., Mon. Myrist. (1897) 268, p.p., for the lectotype only. — *Horsfieldia* sect. *Triavalves* subsect. *Orphanthera* (Warb.) Sincl., Gard. Bull. Sing. 16 (1958) 371, p.p., nom. inval., provisional name only. — lectotype: *Horsfieldia iryagedhi* (Gaertn.) Warb.

Phyllotaxis of plagiotropic shoots distichous. Lower leaf-surface with alveolar tissue, epidermis papillose, stomatal complex sunken; without larger dark coloured

dots (cork warts). Flowers in male sessile, at base not articulate, arranged in many-flowered subglobose dense heads; perianths elongate-obconical, before anthesis \pm angled, 3- or 4- (in ♀ :2- or 4-) valved, splitting the bud to c. 1/2-3/4. Androecium elongate, sub-cylindrical, androphore distinct; central column narrow, narrowly hollowed out for over 1/2-way; anthers 3-5, erect. Stigma sessile, many-lobulate. Ceylon. — Figure 1, I; 2I; species 1.

This section is monotypic with *H. iryagedhi*¹, a species deviating from all other *Horsfieldias* by the following characters: — some anatomical characters of the leaf, the male flowers being sessile and arranged in dense heads which have a thick receptacle, the anthers being mostly connate but in most instances not back to back so that a narrowly hollowed central column is thereby formed, the angular perianths, and the many-lobed (not 2-lobed) stigma in the female flowers.

2. Sect. *Irya* (Hook.f. & Th.) Warb.

Myristica sect. *Pyrrhosa* Bl., Rumphia 1 (1837) 190, p.p., for *M. javanica* and a few other species only, excl. lectotype *M. glabra* (sect. *Pyrrhosa*) and *M. horsfieldii* (= *H. iryagedhi*, sect. *Horsfieldia*); A.DC., Prod. 14 (1856) 202, p.p.; Miq., Fl. Ned. Ind. 1, 2 (1859) 64, p.p., excl. *M. glabra* (= sect. *Pyrrhosa*).

Myristica sect. *Irya* Hook.f. & Thomson, Fl. Ind. (1855) 159; A.DC., Prod. 14 (1856) 202; Miq., Fl. Ned. Ind. 1, 2 (1859) 64; Benth. & Hook.f., Gen. Pl. 3 (1880) 137, p.p., excl. sect. *Horsfieldia*; King, Ann. Roy. Bot. Gard. Calc. 3 (1891) 284, p.p., for the smaller part only. — *Horsfieldia* sect. *Irya* (Hook.f. & Th.) Warb. subsect. *Euirya* Warb., Mon. Myrist. (1897) 123, 267, p.p., for the type only. — Type: *Myristica irya* Gaertn. = *Horsfieldia irya* (Gaertn.) Warb.

Horsfieldia sect. *Pyrrhosa* subsect. *Bivalves* Warb., Mon. Myrist. (1897) 262 (incl. series *Smithii* and series *Globularia*). — *Horsfieldia* sect. *Bivalves* Sinclair, Gard. Bull. Sing. 16 (1958) 370, 371, *comb. inval.*, provisional name only. — Type not indicated, several species listed.

Phyllotaxis in: plagiotropic shoots distichous. Lower leaf surface without alveolar tissue, epidermis not papillose, stomatal complex not sunken; rarely (*H. inflexa*) with larger dark coloured dots. Flowers pedicelled, base not articulate, solitary or in loose clusters; perianth rarely globose or obovoid, usually laterally compressed, in outline either circular or elliptic or pear-shaped, before anthesis not angular or in young stages of *H. sylvestris* faintly so, usually all or predominantly 2-valved, rarely 3-valved, cleft at anthesis to various depths even nearly to the base. Androecium various, nearly always more or less zygomorphic, either usually laterally compressed or in some species with 3- (or 4-) valved flowers, the androecium broad-ellipsoid with the anthers at apex bi-laterally incurved, rarely obconical and actinomorphic; androphore distinct or not, central column broad or narrow, little to much hollowed; anthers few to many, erect or sub-erect, or some or all incurved over or to various depths into the cavity of the central column. Stigma minutely 2-lobed. Mainly E. Malesia (incl. Philippines), only *H. irya* distributed over almost the whole area of the genus. — Figure 1, 6-45; 2 II; species 6-45.

Almost all of the 40 species of this section have exclusively or predominantly 2-valved perianths in the same inflorescence, and usually have a more or less zygomorphic androecium, either because it is laterally compressed or because the anthers curve in apically from two opposite sides only.

Aberrant are *H. olens*¹⁷, *H. sepikensis*¹⁸ with 3- or 4-valved perianths, but with the androecium distinctly tending to be zygomorphic, the anthers from two opposite sides incurved in a manner reminiscent of the condition as found in species like *H. parviflora*, *H. moluccana*; *H. angularis*²⁶ has a 2-4 valved perianth.

Also aberrant are the species of the group of *H. clavata*²², with a 2-lobed perianth but a club-shaped non-zygomorphic androecium.

A few mutually related species from continental SE. Asia, presently placed in the next section, (3) *Pyrrhosa*, viz. *H. longiflora*, *H. thorelii* and *H. amygdalina*

have all or partly predominantly a 2-valved perianth, and partly a zygomorphic androecium, especially *H. longiflora*. This latter species blurs the distinction between sect. *Irya* and sect. *Pyrrhosa*, because, if judged from its morphology of the perianth and androecium, it seems to agree with sect. *Irya*. However, it clearly belongs to the group of the other above-named species, which obviously link up with sect. *Pyrrhosa*. Moreover, since sect. *Irya* is mainly of East Malesian distribution, *H. longiflora* would be occupying an aberrant locality as it is restricted to Indo-China. Compared with other species in sect. *Irya*, *H. irya* extends far beyond their range of distribution; besides, its relationship with *H. longiflora* is rather remote. The phylogenetic backgrounds of this strayed species within sect. *Pyrrhosa*, known only from a few Vietnam collections, pose a problem. Within sect. *Irya*, 8 groups (1—8) can be distinguished.

SURVEY OF GROUPS WITHIN SECT. IRYA

(1) *H. irya*-group

H. irya-group consists of a single species, *H. irya*⁶, which occupies a rather isolated position. It is distinct in habit, with thin leaves often provided with irregular pale blotches, and unique by having globose fruits and seeds, the globose 2-valved male perianth and a typical androecium which is only slightly laterally compressed, and with the anthers almost free, and attached to the rim of the cup-shaped androecium. It is linked with the next group by *H. palauensis*¹⁶ which occupies a rather intermediate position between *H. irya* and *H. smithii*¹⁵.

(2) *H. parviflora*-group, species 7-16

Group 2 is chiefly characterized by the distinctly laterally compressed, male perianth, which is either \pm pear-shaped or circular or more or less transversely elliptic or reniform in lateral view. The laterally compressed androecium follows the shape of the male perianth and consists of anthers connate to various degrees and deeply curved inward into the central cavity at one or both sides of the androecium. This is partly Warburg's sect. *Pyrrhosa*: subsect. *Bivalvis*: series *Globularia* and series *Smithii*.

(3) *H. olens* — *H. sepikensis*-group

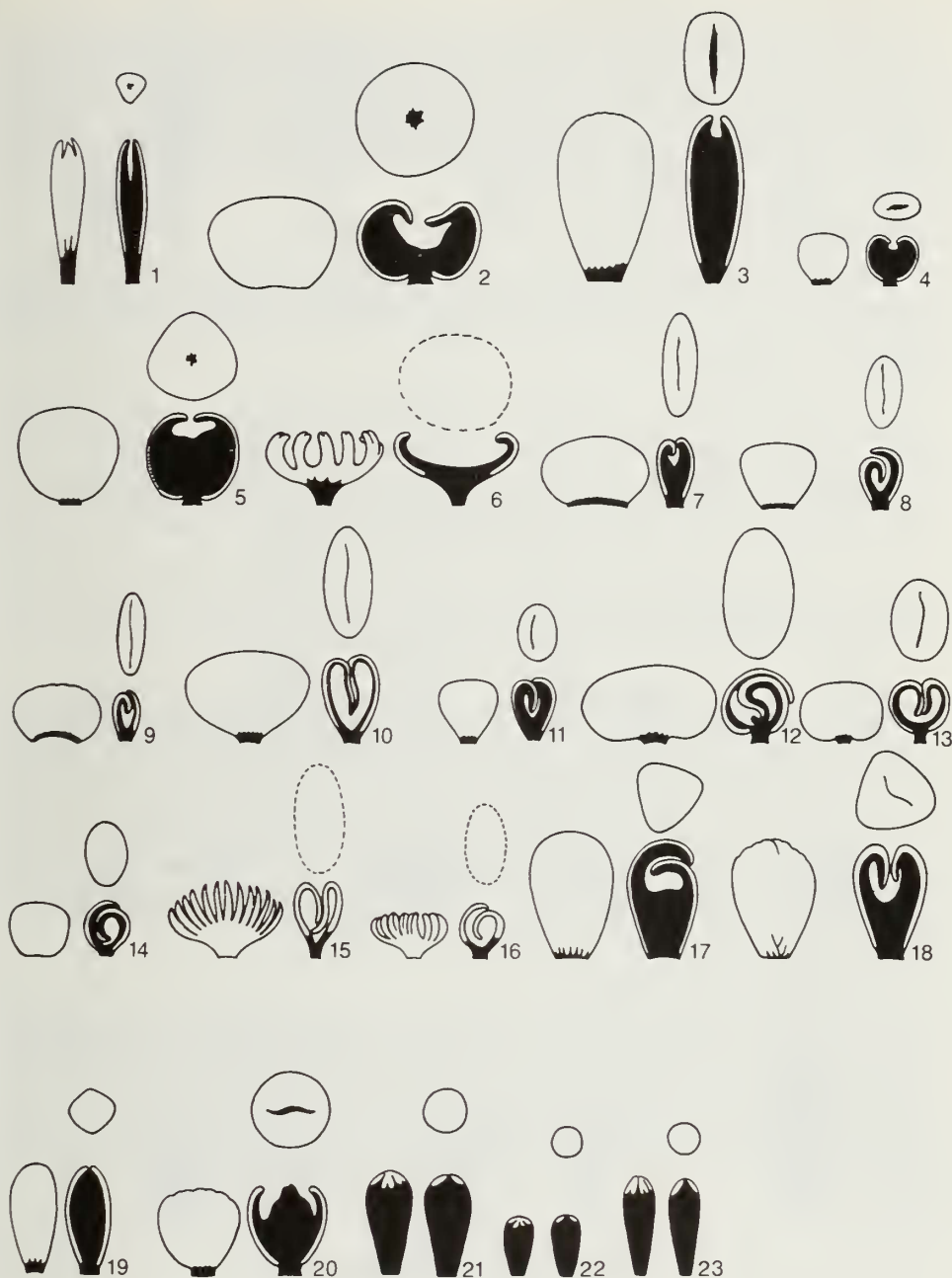
The two species of group 3, 17 and 18, are aberrant in the section because of their 3-valved perianths. The androecium is rather broadly obovoid and only slightly zygomorphic, but the apical parts of the anthers curve inwards \pm bilaterally, in a manner reminiscent of that in the foregoing group.

(4) *H. sylvestris*-group

H. sylvestris-group contains a sole species (16), occupying an isolated position, and is readily recognized by a number of characters. Warburg (1897) placed it with *H. iryagedhi* and *H. ralunensis* in a separate section called *Orthanthera* because the male flowers are elongate and densely clustered in flower heads, but this latter feature only holds for *H. iryagedhi*, because in *H. sylvestris* similar flower heads are only present in juvenile inflorescences, which later on expand into separately attached flowers. The flowers of *H. sylvestris* have an elongate perianth and androecium, not or but little compressed, and the anthers are mutually completely connate forming a narrow, completely solid, central column.

(5) *H. australiana*-group

A rather isolated species, *H. australiana*²⁰, is the sole member. Sinclair had assigned plants from New Guinea to this species but here I accept them as belonging to a distinct species: *H. sinclairii*. In *H. australiana* the androecium is rather broad-ovoid, overarching over a broad and \pm shallow, apical hollow, into which the central column protrudes conspicuously. Based on the flower-features, *H. sinclairii* is assigned to the group of *H. laevigata*³⁵.



Figs. 1A-D Semi-schematic drawings of the androecium of most species of *Horsfieldia*, all depicted except species 24, 55, 62, 76; lateral view (left), longitudinal section (right), apical view (top); white: anthers, black: sterile tissue (i.e. androphore and central column).

Fig. 1A. Species 1-23: 1, *H. iryagedhi* (x 10, Jayasurika & Bandaranaike 1869); 2, *H. kingii* (x 10, Haines 842); 3, *H. longiflora* (x 10, Eberhardt 3050); 4, *thorelii* (x 10, Poilane 19887); 5, *H. amygdalina* var. *lanata* (x 10, Kerr 8556); 6, *H. irya* (x 10, Muller 1020, from Indo-China); 7, *H. spicata* (x 5, Beguin 1407); 8, *H. inflexa* (x 5, LAE 52866); 9, *H. moluccana* var. *moluccana* (x 5, Kostermans 673a); 10, *H. parviflora* (x 5, Ding Hou 134); 11, *H. obscurinervia* (x 5, For. Bur. 26503); 12, *H. ardisiifolia* (x 5, Cuming 1702); 13, *H. talaudensis* (x 5, Lam 2628); 14, *H. samarensis* (x 5, PNH 117374); 15, *H. smithii* (x 5, Rutten 1776); 16, *H. palauensis* (x 5, Takahide Hosakawa 6756); 17, *H. olens* (x 10, NGF 31966); 18, *H. sepikensis* (x 10, Hoogland & Craven 10255); 19, *H. sylvestris* (x 10, Craven & Schodde 739); 20, *H. australiana* (x 5, Dunlop 3585); 21, *H. crux-militensis* (x 5, Schlechter 19246); 22, *H. clavata* (x 5, Hoogland 3663); 23, *H. squamulosa* (x 5, Pullen 8287).

(6) *H. clavata*-group, species 21-23

The three species in the *H. clavata*-group are from New Guinea. They form a distinct group based on various characters dominated by the peculiar club-shaped, not zygomorphic androecium with small sessile anthers at the apex. A thickened sterile androecium with small, apically attached anthers is also found in *H. pulverulenta*, *H. sterilis* and *H. triandra* but in a somewhat different manner. The species of the *H. clavata*-group are shrubs or low trees.

(7) *H. laevigata*-group, species 24-41

The group has mainly species from New Guinea. Several sub-groups can be distinguished, but all are characterized by a laterally compressed perianth and androecium. The anthers are erect and the rather narrow central column is narrowly cleft to various depths.

The two species *H. ampla*²⁴ and *H. ampliformis*²⁵ are characterized by their large male inflorescence and the androphore in *H. ampliformis* is conspicuous.

H. angularis, *H. iriana* and *H. aruana*, species 26-28, are distinct by their ridged or angled twigs; *H. angularis*²⁶ has the male perianth variably 2- to 4-lobed.

*H. subtilis*²⁹ and *H. schlechteri*³⁰ are small trees; both have the androecium rather narrowly stalked with the central column somewhat thickened towards the base, and hence the androecium is often slightly sagged.

Species 31-41 are rather heterogeneous and some have special features:—*H. basifissa*³¹ and *H. sinclairii*³² both have rather small globose or subglobose fruits, but in *H. basifissa* the perianth is deeply cleft; *H. psilantha*³³ comes close to *H. laevigata*³⁵ but its flowers are (almost) glabrous, the leaves are larger, etc., *H. lancifolia*³⁷ and *H. decalvata*³⁸ from Celebes and the Moluccas respectively, stand apart within the present group by their pear-shaped perianth with a tapering pedicel, but, the wide-spread and variable *H. tuberculata*³⁹ usually has somewhat pear-shaped flowers also; *H. corrugata*⁴⁰ and *H. pachycarpa*⁴¹ are mountainous species with very large fruits as compared with the other species of the group.

(8) *H. hellwigii*-group, species 42-45

H. hellwigii-group is restricted to New Guinea and the Bismarck Archipelago, and is generally easily recognized by the rather stout habit (somewhat resembling the wide-spread *H. sylvestris*) and the coarse tomentum on the leaf bud and twig apex; *H. pulverulenta*⁴² is very distinct within this group by the peculiar androecium, which is reduced to a largely sterile cone with 2 minute anthers at the top, and the hard-fleshed perianth which opens apically only by a small slit just above the anthers.

3. Sect. *Pyrrhosa* (Bl.) Warb.

Myristica sect. *Pyrrhosa* Bl., Rumphia 1 (1837) 190-192, Tab. 62-64, p.p., for the smallest part incl. the lectotype Tab. 64, fig. 1A, B; Hook.f. & Thomson, Fl. Ind. (1855) 160; A.DC., Prod. 14 (1856) 202, p.p.; Miq., Fl. Ned. Ind. 1, 2 (1859) 64, p.p.; Benth. & Hook.f., Gen. Pl. 3 (1880) 136; King, Ann. Roy. Bot. Gard. Calc. 3 (1891) 282. — *Horsfieldia* sect. *Pyrrhosa* (Bl.) Warb. subsect. *Eupyrrhosa* Warb., Mon. Myrist. (1897) 265 (excl. *H. macrocoma* = *Endocomia* gen. nov. — Lectotype: *Myristica glabra* Bl. = *H. glabra* (Bl.) Warb.

Myristica sect. *Eumyristica* Hook.f. & Thomson, Fl. Ind. (1855) 162, p.p., for *M. superba* = *Horsfieldia superba* (Hook.f. & Th.) Warb. only. — *Myristica* sect. *Caloneura* A.DC., Prod. 14 (1856) 192, p.p., for *M. superba* Hook.f. & Th. = *Horsfieldia superba* (Hook.f. & Th.) Warb. only.

Myristica sect. *Irya* auct. non Hook.f. & Th; King, Ann. Roy. Bot. Gard. Calc. 3 (1891) 284, p.p.

Horsfieldia sect. *Irya* (Hook.f. & Th.) Warb. subsect. *Euirya* Warb., Mon. Myrist. (1897) 267, p.p., excl. *H. irya* (type).

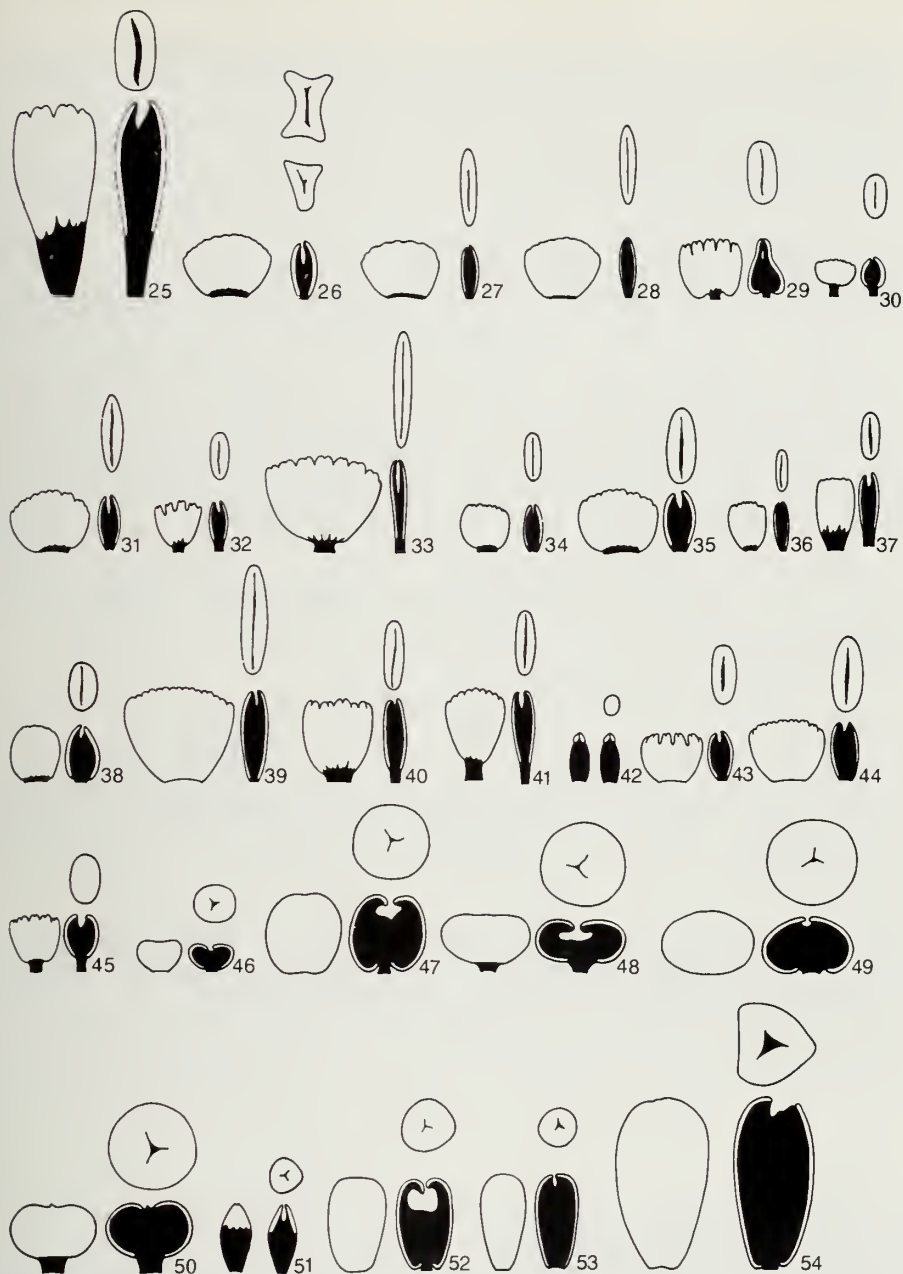


Fig. 1B. Semi-schematic drawings of *Horsfieldia* cont.

Species 24-54: (24, *H. ampla*, male flowers not extant); 25, *H. ampliiformis* (x 10, Hoogland & Craven 11085); 26, *H. angularis* (x 5, Iwanggin BW 5828); 27, *H. iriana* (x 5, Zipelius 139d); 28, *H. aruana* (x 5, Zipelelius s.n.); 29, *H. subtilis* var. *subtills* (x 5, Versteegh & Vink BW 8377); 30, *H. schlechteri* (x 5, NGF 13293); 31, *H. basifissa* (x 5, Womersley 3821); 32, *H. sinclairii* (x 5, NGF 28886, type); 33, *H. psilantha* (x 10, Sands et al. 2047); 34, *H. whitmorei* (x 5, BSIP 7565); 35, *H. laevigata* var. *laevigata* (x 5, Craven & Schodde 874); 36, *H. pilifera* (x 5, Clemens 1710); 37, *H. lancifolia* (x 5, bb. Cel./11. 464); 38, *H. decalvata* (x 5, Idjan & Mochtar 181); 39, *H. tuberculata* (x 5, Waterhouse 820B); 40, *H. corrugata* (x 5, Carr 14123); 41, *H. pachycarpa* (x 5, Manner & Street 307); 42, *H. pulverulenta* (x 5, LAE 43567); 43, *H. leptantha* (x 5, Vink BW 12194); 44, *H. hellwigii* var. *hellwigii* (x 5, NGF 26253); 45, *H. ralunensis* (x 5, NGF 44388); 46, *H. sabulosa* (x 10, SAN 15146, immature); 47, *H. atjehensis* (x 10, Bangham 882); 48, *H. sucosa* subsp. *sucosa* (x 10, SNF 40629); 49, *H. pallidicaula* var. *pallidicaula* (x 10, Hose 29); 50 *H. sparsa* (x 10, FRI 7982); 51, *H. triandra* (x 5, Forbes 2465); 52 *H. tristis* (x 5, S 37470); 53, *H. fulva* (x 5, KEP 99334); 54, *H. superba* (x 5, FRI 4511).

Horsfieldia sect. *Irya* (Hook.f. & Th.) Warb. subsect. *Trivalves* Warb., Mon. Myrist. (1897) 267. — *Horsfieldia* sect. *Trivalves* subsect. *Trivalves* Sinclair, Gard. Bull. Sing. 16 (1958) 370, 371, *comb. inval.*, provisional name only. — Type not indicated.

Horsfieldia sect. *Orthanthera* Warb., Mon. Myrist. (1897) 268, p.p., for *H. ralunensis* and *H. sylvestris* only, excl. the lectotype *H. iryaghedhi*.

Phyllotaxis of plagiotropic shoots dispersed or distichous. Lower leaf surface without alveolar tissue, epidermis not papillose, stomatal complex not sunken; with or without larger dark coloured dots or cork warts. Flowers with a pedicel (short in *H. wallichii*), at base with or without articulation, solitary or in loose clusters; perianth (depressed) globose, or obovoid or ellipsoid, not laterally compressed, not or but faintly angular, generally perianths all or predominantly 3- (or 4-) valved, rarely 2-valved (*H. longiflora*, *H. sterilis*), cleft at anthesis to c. 2/3 or less. Androecium actinomorphic or more or less triquetrous in transverse section, never laterally compressed, depressed-globose or ellipsoid or obovoid, usually with a broad central column with an apical hollow of various shape and depth; androphore short or rather long, usually narrow at base; anthers various in number, \pm straight or curved, either almost entirely connate or \pm straight-erect and mutually free for about the upper half (*H. polyspherula*-group). Stigma minutely 2-lobed. Continental SE. Asia, West Malesia (incl. Philippines). — Figures 1, 2-5, 46-100; 2 III; species 2-5, 46-100.

This section of 59 species contains mainly those with exclusively or predominantly a 3- (or 4-) valved perianth, the rest are 3 species with a 2-valved perianth, viz., *H. longiflora* from Vietnam, *H. crassifolia* (Malaya, Sumatra, Borneo) and *H. sterilis* from Sabah. I believe that these exceptions should be placed among the species of the present section *Pyrrhosa* as is briefly discussed in the notes to the preceding section for *H. longiflora*, and argued for *H. crassifolia* and *H. sterilis* below.

Within sect. *Pyrrhosa* some 15 groups (9-23) can be distinguished, some of them are heterogeneous, others have a clear circumscription particularly the *H. polyspherula*-group or contain only a single aberrant species.

SURVEY OF GROUPS WITHIN SECT. PYRRHOSA

(9) *H. amygdalina*-group, species 2-5

Group 9 clearly links up with the *H. glabra*-group (sp. 97-100) because of the largely identical construction of the male flowers, and the phyllotaxis which is either distichous or dispersed, but differs in the absence of cork warts on the lower leaf surface. The group is keyed out at the beginning: — because it has a distinct distributional area in continental SE Asia, and because of the variable number of perianth-valves (2-4) and the variable phyllotaxis, and this situation rather interferes with the keying out of most of the West Malesian species, which are clearly distinctive. *H. kingii* is readily distinguished by its pubescent, 4-valved male perianth.

(10) *H. sabulosa*-group

Group 10 consists only of *H. sabulosa*⁴⁶, which, from the study of the rather immature male flowers, links up with the group of e.g. *H. borneensis*⁸⁵ or *H. punctata*⁹⁰. It is however readily distinguished by its ramiflorous flowering, dispersed phyllotaxis, long-petioled leaves, dark-coloured dots or stripes on the lower leaf surface, etc. The leaves have an iso-bilateral anatomy as was discovered by Koster and Baas (1981).

(11) *H. pallidicaula*-group, species 47-50

The species in group 11 are usually easily distinguished by the pale, grey-brown or straw-colour of the dried twigs, contrasting with the blackish colour of the dried leaves. Usually the flowers, leaves and fruits also dry to a relatively black colour. The phyllotaxis is mostly dispersed. In *H. sucosa*⁴⁸ and *H. pallidicaula*⁴⁹p.p. the calyx remains persistent under the fruit; *H. atjehensis*⁴⁷ is distinct by the presence of blackish brown dots or cork warts on the lower leaf surface. The architecture of the androecium of this group links up with that of many other species, e.g., the *H. glabra*-group. In *H. sucosa* subsp. *bifissa*^{48b} the perianth is predominantly 2-valved, which is aberrant in the present section.

(12) *H. triandra*-group

Group 12 consists of a single species, *H. triandra*⁵¹, from C. and S. Sumatra, and is distinct by flowers in that the perianth is thick-leathery and opens by 3 valves split to only c. 1/5, and in the turbinate androecium, with 3 reduced anthers at the top. Similar androecia with 'reduced' anthers occur in e.g., *H. sterilis*, *H. pulverulenta*, and the *H. clavata*-group of sect. *Irya*, but I doubt that these species are otherwise related.

(13) *H. fulva*-group, species 52-54

These three species occupy a separate position because of the leaves drying to a dull colour above. The male perianth and androecium are of an elongated shape. In *H. fulva* and *H. superba* the perianth remains persistent under the fruit.

(14) *H. sessilifolia*-group

Group 14 consists of a possibly isolated species (55), characterized by the almost-sessile leaves; its male flowers are not known.

(15) *H. grandis* — *H. motleyi*-group, species 56-60

Group 15 is named here merely for convenience, as its five constituents, *H. grandis*⁵⁶, *H. wallichii*⁵⁷, *H. pulcherrima*⁵⁸, *H. flocculosa*⁵⁹, *H. motleyi*⁶⁰ all differ considerably from each other in general habit as well as the shape of the male perianth and especially the androecium. Only *H. grandis* and *H. pulcherrima* seem more closely related according to the male flowers, but for the rest, all five species could represent separate groups as well. *H. flocculosa*⁵⁹ has a somewhat elongated male perianth and an elongate androecium, and therefore suggests connections with the *H. fulva*-group.

(16) *H. affinis*-group, species 61-67

Group 16 is characterized by a globose or depressed globose androecium with a moderate apical hollow, and a short and slender androphore; in these it seems much related to the group of *H. endertii* — *H. montana* (83-89). Our present group, however, is segregated by a generally persistent tomentum on the lower leaf-surface. *H. affinis*⁶⁶ and *H. reticulata*⁶⁷ have very distinctly articulated pedicels.

(17) *H. crassifolia*-group

Group 17 consists of only one species, *H. crassifolia*⁶⁸, which deviates in many respects viz., a 2-valved perianth, an actinomorphic subglobose androecium with largely free anthers (fig. 1C), a persistent perianth under the fruits and a dotted lower leaf surface. The pedicels at the base are not articulated. Because of the largely free anthers and the 2-valved perianth, this species may have affinity to the wide-spread *H. irya*⁶ from section *Irya*.

(18) *H. carnos*a-group

Group 18 possibly should not have been mentioned as a group, because its single species (69) links up with species from the group of *H. borneensis*⁶⁵ by its male

flowers. Vegetatively and ecologically (heath forest, peat swamp forest) it is, however, quite distinct.

(19) *H. sterilis*-group

The position of group 19, with its single species *H. sterilis*⁷⁰ from SE. Sabah is problematic within section *Pyrrhosa*. Its perianths are 2-valved, opening at anthesis only at the very apex; the androecium is, however, actinomorphic, i.e., faintly blunt-triangular, and consists of a large sterile conical part with 6 anthers apically attached (or possibly 3 anthers each with 2 thecae). It has twigs drying rather pale and with dark leaves and is hence vegetatively reminiscent of the *H. pallidicaula*-group with which it has no affinity if judged from the androecium. The female perianth persists under the young fruit.

(20) *H. polyspherula*-group, species 71-82

Group 20 is remarkably coherent on account of the following characters: pedicels articulated at the base, androecium (generally) triquetrous in transverse section, anthers suberect and mutually free for about the upper half; furthermore, most species (except *H. ridleyana*⁷⁴) have the lateral nerves distinctly raised above. The group can be divided in 2 subgroups based on whether the internodes are distinctly ridged (or short-winged) or angular as in species *H. hirtiflora*⁷¹ and *H. brachiata*⁷², respectively. In *H. hirtiflora*, a rather deviating species with its pubescent 4-valved perianth, and leaves partly dispersed, the androecium is rather roundish, not triquetrous in section, but the erect and largely free anthers still point to a relationship within the *H. polyspherula*-group. This group correlates with Warburg's sect. *Irya* subsect. *Trivalves*.

(21) The group of *H. endertii*⁸³, *H. valida*⁸⁴, *H. borneensis*⁸⁵, etc. to *H. obscura*⁹³ (spec. 83-93) is rather heterogeneous, but most of its species are clearly interrelated as they have in common a depressed globose narrowly-stalked androecium with a moderately deep, apical hollow. In *H. fragillima*⁸⁶ this hollow is exceedingly broad, rendering the androecium saucer-shaped; in *H. androphora*⁸⁷ the androphore is conspicuously elongated; *H. borneensis*⁸⁵ has distinctly articulated pedicels and on the lower leaf surface blackish marks, presumably cork warts. Through *H. punctata*⁹⁰, with a dotted lower leaf surface, there is a strong connection of the present group with the group of *H. glabra*¹⁰⁰. Species 83-89 all have in common a coarse tomentum on the leaf bud. Through its coarse pubescence *H. endertii*⁸³ leads the present group though it deviates by its elongate male perianth and androecium, which it shares with the species of the next group.

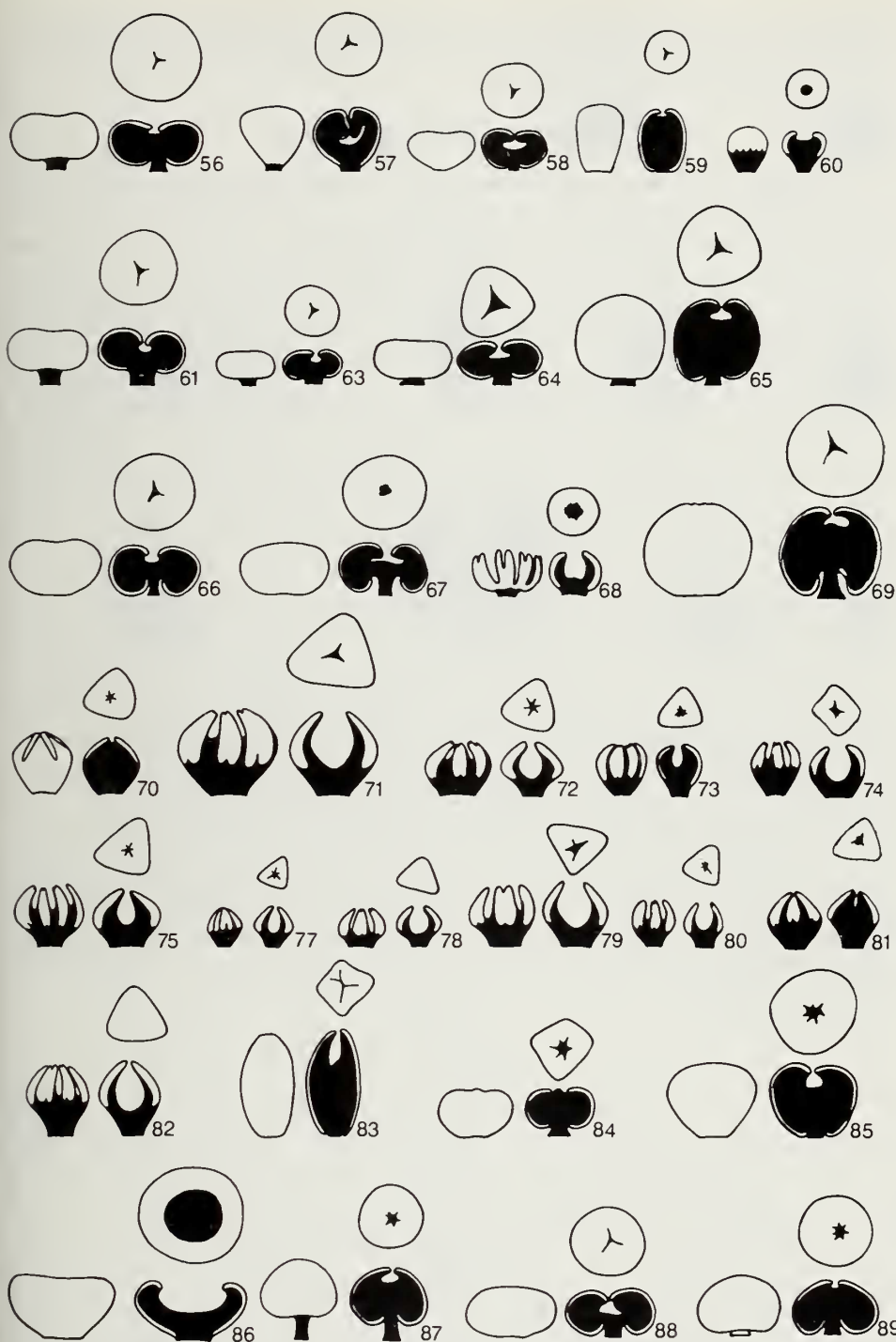
(22) *H. xanthina*-group, species 94-96

Species of group 22 and *H. endertii*⁸³ of the foregoing group have in common an elongate male perianth and androecium. Whether these species are in reality more

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Fig. 1C. Semi-schematic drawings of *Horsfieldia* cont.

Species 55-89: (55, *H. sessilifolia*, male flowers not known); 56, *H. grandis* (x 10, Chew Wee-lek 261); 57, *H. wallichii* (x 5, FRI 12135); 58, *H. pulcherrima* (x 10, FRI 8008); 59, *H. flocculosa* (x 5, KEP 110225); 60, *H. motleyi* (x 10, Kostermans 6859); 61, *H. tomentosa* (x 10, FRI 15957); 62, *H. gracilis*, male flowers not known); 63, *H. paucinervis* (x 10, Haviland 3075); 64, *H. splendida* (x 10, S 33723); 65, *H. rufo-lanata* (x 10, Richards 1667); 66, *H. affinis* (x 10, S 24718); 67, *H. reticulata* (x 10, Hans Winkler 388); 68, *H. crassifolia* (x 10, SFN 40898); 69, *H. carnososa* (x 10, van Niel 4519); 70, *H. sterilis* (x 10, SAN 30597); 71, *H. hirtiflora* (x 10, Rahmat si Boeea 9257); 72, *H. brachiata* (x 10, King's Coll. 4704); 73, *H. pachyrachis* (x 10, bb. 28128); 74, *H. ridleyana* (x 10, Scortechini 12); 75, *H. obtusa* (x 10, Native Coll. BS 821); 76, *H. disticha*, male flowers not known); 77, *H. tenuifolia* (x 10, S 24945); 78, *H. macilenta* (x 10, B.N.B. 4204); 79, *H. laticostata* (x 10, S. 17252); 80, *H. nervosa* (x 10, S 16652); 81, *H. polyspherula* var. *polyspherula* (x 10, KEP 38129); 82, *H. oligocarpa* (x 10, Ashton & Whitmore BRUN 398); 83, *H. endertii* (x 5, Ender 3996); 84, *H. valida* (x 5, Lorz 5896); 85, *H. borneensis* (x 10, S 14610); 86, *H. fragillima* (x 10, Bakar S 4361); 87, *H. androphora* (x 10, S 35443); 88, *H. anplomontana* (x 10, SAN 18843); 89, *H. montana* (x 10, Sinclair 8987).



closely inter-allied remains uncertain. The androecium of *H. majuscula*⁹⁵ is triquetrous in section and the pedicel is articulated at the base, and therefore this species might be close to the *H. polyspherula*-group (species 71-82).

(23) *H. glabra*-group, species 97-100

As already mentioned under the *H. amygdalina*-group (spec. 2-5), and e.g., also in the comments on *H. punctata*⁹⁰, *H. glabra*-group has several connections with others, especially in its largely similar, subglobose or ellipsoid androecium with a

smallish apical cavity. The group is readily distinguished by the very short tomentum of the leaf bud and of the inflorescence, and by the presence of dark-coloured dots, i.e. cork warts, on the lower leaf surface.

Geographical Distribution

Horsfieldia, with 100 species, ranges from Ceylon through NE. India to S. China (Kwangsi, Hainan) and through Malesia and the Caroline Isls. east to the Solomon Isls. and N. Australia. It is absent from the Lesser Sunda Isls. Apart from a few widely distributed species, e.g., *H. irya*, *H. glabra*, *H. amygdalina*, *H. laevigata*, or *H. tuberculata*, most species are of limited distribution. Distinct centres of species-development are New Guinea and Borneo, and to a lesser extent Malaya-Sumatra. Here recognized are three sections, which occupy largely mutually exclusive areas. Section *Horsfieldia*, with only *H. iryaghedhi*, is confined to Ceylon. Section *Irya* (with 40 species) is, except for the wide-spread *H. irya* (see fig. 2), confined to E. Malesia and the Solomon Isls. and N. Australia, as indicated in figure 2. The section *Pyrrhosa* occurs west of Wallace's Line as also indicated in that figure by a broken line. In distribution, Sections *Irya* and *Pyrrhosa* overlap for a relatively narrow area in the Philippines and Celebes. They are segregated mainly because of a different valve-number of the perianths viz., predominantly 2 in the east-occurring sect. *Irya* and predominantly 3 in the west-occurring sect. *Pyrrhosa*. Some species with the perianth-valve number deviating from that in the section but still regarded as belonging to it are for sect. *Irya*: *H. olens*¹⁷, *H. sepikensis*¹⁸, and *H. angularis*²⁶. In the west-occurring section *Pyrrhosa* the deviating valve number 2 is found in: *H. longiflora*³, *H. thorelii*⁴ (and *H. amygdalina*⁵, for a minor part), *H. crassifolia*⁶⁸ (see fig. 2) and *H. sterilis*⁷⁰. Why these species are better listed in this section is briefly explained in the foregoing chapter in the discussion on sections and groups. Apart from these few species with a deviating valve-number, the division into the sections *Pyrrhosa* and *Irya* based on the character of the perianth being 3- and 2-valved respectively, correlated with their respective different geographical distribution is peculiar because in most individual specimens the number of perianth-valves is not at all constant: perianths with a deviating valve-number are usually found in low percentages. In general, however, though not strictly constant, even in the specimens, the character of the predominant valve-number has apparently some phylogenetic significance connected with Wallace's Line.

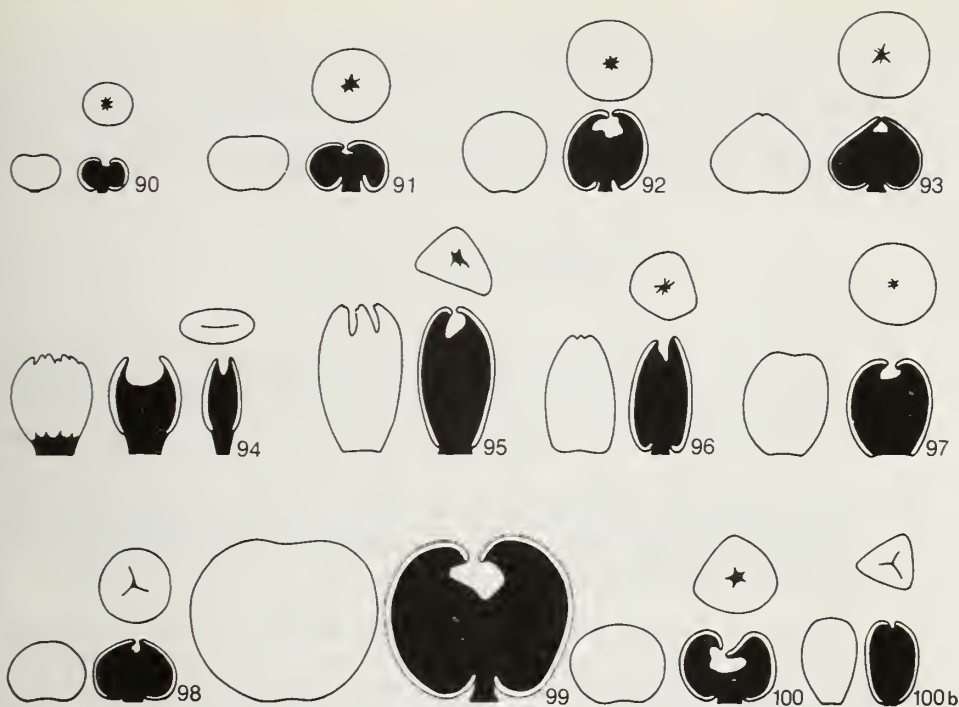


Fig. 1D. Semi-schematic drawings of *Horsfieldia* cont.

Species 90-100b: 90, *H. punctata* (x 10, FR1 9014, slightly immature); 91, *H. costulata* (x 10, PNH 2685); 92, *H. subalpina* subsp. *subalpina* (x 10, Whitmore FR1 3884); 93, *H. obscura* (x 10, Kostermans 13773); 94, *H. xanthina* subsp. *xanthina* (x 10, Richards 1927); 95, *H. majuscula* (x 10, Ramat si Boeea 8772); 96, *H. coriacea* (x 10, bb. Cel. 111/-27); 97, *H. penangiana* (x 10, Curtis 2406 in BM); 98, *H. punctatifolia* (x 10, S 36580); 99, *H. macrothyrsa* (x 10, Lorzing 17195); 100, *H. glabra* var. *glabra* (x 10, Nengah Wirawan 95); 100 b, *H. glabra* var. *javanica* (x 10, Koorders 21635 β).

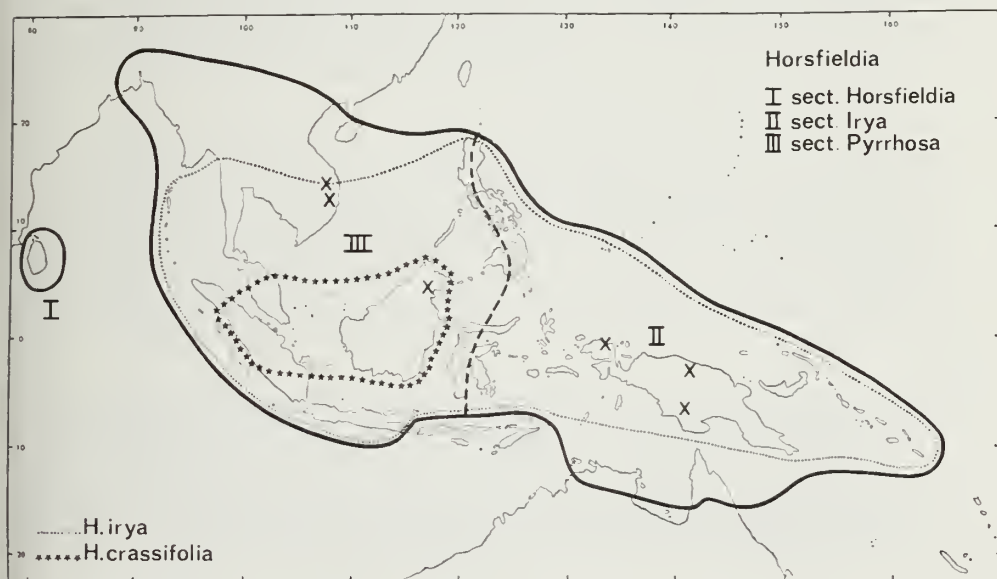


Fig. 2. Distribution of *Horsfieldia*

I. sect. *Horsfieldia* (1 species). — II. sect. *Irya*, 40 species, distributed east of Wallace's Line as drawn by broken line; distribution of *H. irya* as stippled line — III. sect. *Pyrhosa*, 59 species, distributed west of Wallace's Line. Crosses indicate the approximate localities or areas of species with valve-number of perianth straying from the sections. For further explanation see the text.

Keys to the Species

Seven keys are presented, a general key (1) to all species of *Horsfieldia*, based on male flowering specimens, and six regional keys (2-7) for female flowering and fruiting specimens, based partly on vegetative characters and partly on distribution.

(1) GENERAL KEY TO THE SPECIES

based on male flowering specimens

- 1a. *Male flowers sessile*, packed into dense subglobose capitula; perianths \pm obconical, in bud mutually appressed and angular. Male perianth 3-valved, at anthesis cleft to c. 1/5-2/3. Androecium stalked, anthers 3-5. Leaves papillose beneath. *Ceylon, elsewhere cultivated*..... **H. iryaghedhi**¹
- b. Male flowers subsessile or usually pedicelled; perianths various, in bud not or only somewhat angular, mutually free or at least not densely clustered (perianth densely clustered before anthesis in *H. sylvestris* from *E. Malesia*). Leaves not papillose beneath 2
- 2a. Phyllotaxis of plagiotropic (fertile) twigs distichous. Leaves membranous, usually with largish whitish marks of irregular shape and size. Male perianth 2-valved, globose, c. 1-1.5 (-2.0) mm diam. Androecium not or hardly laterally compressed; androphore distinct, tapering, broad above and hollowed to a saucer-shape, shallowly to deeply; anthers 6-10, their apices free for only c. 0.3 mm and \pm in-curved. *Ceylon to Solomon Isls., generally not too far from the coast* **H. irya**⁶
- b. Phyllotaxis of plagiotropic twigs either distichous (alternate), or dispersed (spirally), or mixed in the same specimen. Leaf consistency various, usually, without whitish marks. Male perianth 2-4 valved, various in shape and size. Androecium various, but if the hollow deeply cup- or saucer-shaped then the anther-apices either mutually free for at least 1/2-way, or the anthers strongly inflexed into the cup (anthers connate or mutually free, number of anthers few to many) 3
- 3a. Perianths in any one inflorescence either 2- and 3-valved evenly mixed, or all the flowers with perianths either 2-, or 3-, or 4-valved. Phyllotaxis of plagiotropic (fertile) twigs at least partly dispersed (1/3-2/5 spiral), except in *H. longiflora* (*Annam*) with leaves distichous (always?). Leaves without brown or blackish dots of non-traumatic origin (lens!) beneath. Dried twigs dark brown, not pale and not much contrasting with the colour of the petioles. *Continental SE. Asia, Andaman Isls., not S. of the Isthmus of Kra* 4
- b. Perianths either 2-, or 3-, or 4-valved, the valve number in flowers of any one specimen constant or almost so; sometimes a few flowers excepted. Phyllotaxis distichous or dispersed. Leaves with or without dark dots beneath. Dried twigs straw or grey (pale) to dark brown, much contrasting with the dark colour of the dried petioles or not. *Peninsular Thailand through Malesia to Solomon Isls. and N. Australia* 7
- 4a. Perianths (2- or) 3- or 4-valved, pubescent, in male c. 3.0-4.0 mm diam. **H. kingii**²
- b. Perianths either 2-, or 3-valved, or 2 and 3 valves mixed, outside glabrous, in male c. 1.0-3.0 mm long 5

- 5a. Phyllotaxis of plagiotropic shoots (fertile) distichous (always?). Male perianth \pm elongate-ellipsoid, 2.2-3.0 mm long. Androecium ellipsoid, c. 2.0 mm long. *Annam* **H. longiflora**⁷
- b. Phyllotaxis, usually at least partly, dispersed. Male perianth shorter, c. 1.0-2.3 mm long. Androecium depressed-globose to obovoid, rarely ellipsoid, c. 0.6-2.0 mm long 6
- 6a. Male perianth subglobose or depressed-globose, 1.0-1.5 (-1.7) mm long. Anthers 7-10. *Thailand, Laos, Cambodia, Vietnam: Annam, Cochinchina* **H. thorelii**⁴
- b. Male perianth short-ellipsoid, or subglobose, or obovoid, c. 1.5-2.3 mm long. Anthers 8-15. *S. China, Indo-China (excl. Annam, Cochinchina) NW. to Assam, Andaman Isls. (2 vars.)* **H. amygdalina**⁵
- 7a. Perianths predominantly 2-valved, or sometimes a few flowers in an inflorescence 3- or 4-valved. *Species mainly from E. of Wallace's line, or the following from W. Malesia: H. crassifolia (Malaya, Singapore, Sumatra, Borneo), H. penangiana, p.p. (Sumatra), H. sterilis (Borneo), H. sucosa subsp. bifissa (Borneo)* 8
- b. Perianths predominantly 3-valved, or predominantly 4-valved, or both 3 and 4 valves present; sometimes the odd flower in an inflorescence has a 2-valved perianth. *Species from W. Malesia and penins. Thailand, and the following from New Guinea: H. angularis, H. olens, H. sepikensis* 48
- 8a. Androecium not laterally compressed, in transverse section \pm circular; never distinctly longer than wide. *W. Malesia* 9
- b. Androecium laterally compressed or not; if not or only slightly then the androecium including androphore longer than wide; androecium not or little laterally compressed in occasional 3- or 4-valved flowers. *E. Malesia: Moluccas to Solomon Isls., N. Australia* 12
- 9a. Leaves coriaceous, with inconspicuous, subpersistent, dense tomentum of stellate-scaly hairs with scattered emergents beneath (in specimens of *Borneo* the hairs often deciduous, leaving distinct scars); leaves with scattered brown or blackish dots or streaks (lens!) beneath. Colour of dried twigs and of petioles not much contrasting. *Peat swamp forest, swampy forest on sandy soil* **H. crassifolia**⁶⁸
- b. Leaves \pm membranous, glabrous or early glabrescent beneath. *Not from peat swamp forest* 10
- 10a. Twigs slender, towards apex c. 2 mm diam.; bark not drying to a pale colour. Leaves small, c. 7-12 cm long, with regularly scattered dark dots beneath; lateral nerves flat and inconspicuous above **H. penangiana**⁹⁷
- b. Twigs towards apex c. 2-5 (-10) mm diam.; bark usually drying to a pale colour and contrasting with the blackish dried petioles or not. Leaves 14 cm long or more, not dotted beneath 11
- 11a. Androecium depressed-globose, largely consisting of anthers; central-apical cavity flat and shallow **H. sucosa** subsp. **bifissa**⁴⁸
- b. Androecium broadly obovoid, consisting of a large sterile base, and an upper half bearing 3 (or 6?) inconspicuous anthers **H. sterilis**⁷⁰

- 12a. Male inflorescence spike-like, i.e., either not so or but slightly so and short-ramified, lateral branches up to 5 mm long. Inflorescences, flowers and petioles drying blackish, usually contrasting with the paler grey-brown dried twigs. Anthers inflexed inwards. *Moluccas* **H. spicata**⁷
- b. Male inflorescence usually ramified, the side branches at least 5 mm long. Inflorescences, flowers, and petioles drying brownish or blackish, usually not contrasting with the colour of the dried twigs 13
- 13a. Androecium \pm cup-, or bowl-, or saucer-shaped, moderately laterally compressed; the anthers at one or both sides of the androecium distally distinctly incurved or inflexed into the cup-shaped central cavity. *E. Malesia: Philippines, Celebes, Moluccas, NW. New Guinea, Palau Isls.* 14
- b. Androecium laterally flattened or not, the central column either (1) solid, or at apex, (2) broadly but shallowly hollowed only up to c. 1/3, or (3) narrowly channelled like a slit to various depths; the anthers straight or only slightly in curved, never inflexed into the cup-shaped central cavity. *E. Malesia: Moluccas to Solomon Isls., N. Australia* 22
- 14a. Leaves below with regularly spaced reddish-brown to brown-black dots presumed to be non-traumatic cork warts originating from hair-scars (lens!), not to be confused with a much finer punctuation if also present. Twigs angular or ridged especially in the upper portion **H. inflexa**⁸
- b. Leaves without dots. Twigs either terete, or angular, or winged 15
- 15a. Male perianth together with the pedicel \pm pear-shaped, the pedicel tapering. Petiole relatively long, c. 1.0-2.6 cm, leaf blade (6-) 8-22 (-25) cm. Twigs at apex generally terete, not angular **H. moluccana**⁹
- b. Perianth (in laterally view, on the broad side) either short-cuneate, or rounded, or subtruncate at base; the pedicel not tapered, \pm abruptly passing into the perianth. Petioles generally shorter. Twigs terete or angular 16
- 16a. Anthers entirely connate; androphore short or absent. Male perianth at anthesis cleft to c. 1/2-way 17
- b. Anthers or thecae mutually free at least in the incurved or inflexed portion. Male perianth at anthesis cleft to c. 2/3 or over 18
- 17a. Anthers 18-25, usually inflexed at both sides of the laterally compressed androecium into the thin-walled androecium-cup. Male perianth 2.5-4 mm wide. Leaves membranous, drying matt. *Moluccas* **H. parviflora**¹⁰
- b. Anthers 11-12, usually inflexed at only one side of the androecium-cup; the cup thick- and firm-walled. Male perianth c. 2-2.2 mm wide. Leaves chartaceous, \pm glossy above. *Philippines: Luzon* **H. obscurinervia**¹¹
- 18a. Anthers mutually free only in the inflexed distal portions, the basal non-inflexed portions connate into a cup-shaped androecium. Androphore minute, only c. 1/10 of the androecium-length 19
- b. Anthers free for at least 2/3. Androphore relatively large, its length c. 1/3 of the androecium-length 21
- 19a. Twigs angular or winged. Male perianth c. 4 mm wide, glabrous. *Philippines* **H. ardisiifolia**¹²
- b. Twigs terete, neither ridged nor winged. Male perianth 2.5-3 mm wide ... 20

- 20a. Pedicel of male flowers pubescent, shorter than the perianth. Inflorescences rather densely finely pubescent. Anthers inflexed at both sides of the laterally compressed androecium. *Talaut Isls* **H. talaudensis**¹³
- b. Pedicels of male flowers glabrous, longer than the perianth. Inflorescences sparingly pubescent with hairs less than 0.1 mm long. Anthers inflexed only at one side into the androecium-cup. *Philippines: Samar Isls.* **H. samarensis**¹⁴
- 21a. Twigs generally angular or ridged. Male perianth c. 3-4 mm wide; pedicel glabrous. Anthers all inflexed into the centre of the androecium. *Moluccas* **H. smithii**¹⁵
- b. Twigs terete, usually lined. Male perianth c. 2-2.5(-3) mm wide; pedicel pubescent or glabrescent. Anthers deeply inflexed at one side of the androecium, always partly covered over by those of the other side. *Palau Isls.* **H. palauensis**¹⁶
- 22a. Male perianths angular before anthesis, arranged into dense semi-globose clusters. Androecium much longer than wide, not or but slightly laterally compressed. Leaves lanceolate to lanceolate-linear, usually \pm parallel-sided **H. sylvestris**¹⁹
- b. Flowers not densely clustered, not angular in mature buds 23
- 23a. Mature male perianth either \pm lengthwise ellipsoid, or subglobose, c. 2-3 mm long, very thinly pubescent; at anthesis cleft to c. 1/2-way. Androecium only slightly laterally compressed, the central column broad, broadly hollow in the apical portion, but the central column protruding centrally into this cavity. *Australia* **H. australiana**²⁰
- b. Male perianth various. Central column of androecium not protruding. *E. Malesia, Pacific* 24
- 24a. Twigs sharply angular, or markedly ridged, or winged from petiole to petiole at the apex of the twig as well as lower down in between the older leaves and in older wood; i.e., twigs not merely more or less distinctly lined 25
- b. Twigs not winged, i.e., terete or only somewhat angular at apex, lower down terete or merely provided with lines from petiole to petiole (the bark striate or not) 27
- 25a. Male perianth either 2-, or 3-, or 4-valved, subspherical, hardly or not laterally compressed, drying \pm glossy, not collapsing on drying. *New Guinea: Vogelkop penins.* **H. angularis**²⁶
- b. Male perianth predominantly 2-valved, little or much laterally compressed, drying matt, slightly or strongly collapsing on drying 26
- 26a. Leaves thinly coriaceous. Pedicels of male flowers about as long as or longer than the perianth. Perianth at anthesis cleft almost to the base. Hairs of inflorescence and pedicels c. 0.2-0.3 mm. Anthers 10-14; the central column of androecium at apex hollow for c. 1/4 **H. iriana**²⁷
- b. Leaves membranous. Pedicel shorter than the perianth. Perianth at anthesis cleft to c. 2/3-3/4. Inflorescences and pedicels almost glabrous, with hairs of c. 0.1 mm or less. Anthers (12-) 14-18; the central column of androecium solid or almost so **H. aruana**²⁸
- 27a. Male inflorescence large, 25-35 cm long. Male perianth \pm pear-shaped. Androecium longer than broad; androphore c. 0.5 mm long or more, about

- half as long as the anthers or longer 28
- b. Male inflorescences c. 20 cm long or less. Male perianth of various shapes. Androecium longer or shorter than broad; androphore short or long 29
- 28a. Male perianth glabrous (?), c. 4×2 mm. Anthers 10, androphore nearly as long as the anthers. Inflorescence glabrescent, to 25 cm long **H. ampla**²⁴
- b. Male perianth pubescent, c. 3×3 mm. Anthers 7, androphore about half as long as the anthers. Inflorescence pubescent, c. 25-35 cm long **H. ampliformis**²⁵
- 29a. Male inflorescence delicate, 2-5(-8) cm long, 1 or 2 (or 3) times ramified. *New Guinea, incl. Aru Isls.* 30
- b. Male inflorescences generally stouter, c. 5-20 cm long, not or 1-4 times ramified (inflorescences of *H. sinclairii* and *H. basifissa* from New Guinea sometimes small). *Whole of E. Malesia, incl. Celebes, Pacific; not in the Philippines* 34
- 30a. Male perianth pubescent or late glabrescent, distinctly or only somewhat longer than broad. Anther-bearing part of the androecium much shorter than the elongate club-shaped androphore 31
- b. Male perianth glabrous or early glabrescent, about as long as or shorter than broad. Androphore much shorter than the anthers 33
- 31a. Leaves broadly obovate or elliptic to oblong, c. $12-17 \times 5-11$ cm. Male perianth gradually passing into the thick and tapered pedicel, both together c. 10-12 mm long. Androphore glabrous **H. crux-melitensis**²¹
- b. Leaves elliptic to lanceolate, $4.5-20 \times 0.7-6$ cm. Male perianth with pedicel 4-6(-9) mm 32
- 32a. Leaves drying olivaceous. Male perianth with pedicel together club-shaped, c. $5-5.5 \times 2-2.2$ mm. Androphore glabrous **H. clavata**²²
- b. Leaves drying dark brown. Male perianth broadly ellipsoid, c. $2.0-2.4 \times 1.8-2.2$ (-2.4) mm, at base narrowed into a slender pedicel 2-3.5(-6) mm. The surface of the androphore in the upper part wrinkled-bullate, towards the base either densely, minutely scaly-hairy, or striate but glabrous **H. squamulosa**²³
- 33a. Male perianth \pm laterally compressed, generally \pm obtriangular in lateral view, 1.8-3 mm wide, usually \pm collapsing on drying. Androphore slender, c. 0.2-0.5 mm long, usually much shorter than the anthers **H. subtilis**²⁹
- b. Male perianth generally subglobose, 1-2 mm wide, not or but slightly compressed, the surface wrinkled on drying but not collapsing. Androphore 0.4-0.5 mm long, about half the length of anthers **H. schlechteri**³⁰
- 34a. Male perianths together with the pedicels generally \pm pear-shaped; the upper part of the perianth broadly rounded in lateral view, the lower (1/4-) 1/3-1/2 tapered and gradually passing into the \pm tapered pedicel (these characters not always clear in certain specimens of *H. tuberculata*). Perianth glabrous, pubescent or glabrescent 35
- b. Male perianth in lateral view of various shapes, either circular, or ovate, or obovate, or elliptic, or transversely elliptic, or reniform; at base either

- short-attenuate, or rounded, or truncate; not tapered, the pedicels generally not thickened towards the perianth. Perianth either hairy, at least at the base, or in *H. psilantha*, *H. basifissa*, *H. sinclairii* glabrous, subglabrous, or glabrescent 39
- 35a. Perianth glabrous. *A variable species* ***H. tuberculata***³⁹
- b. Perianth minutely pubescent, or early glabrescent in *H. corrugata* 36
- 36a. Leaves small, \pm lanceolate, 5-16 cm long. Male perianth at anthesis cleft to only c. 1/6. *Celebes* ***H. lancifolia***³⁷
- b. Leaves elliptic to lanceolate, generally much larger, 12-30 cm long. Male perianth at anthesis cleft to c. 1/2-way 37
- 37a. Pedicel c. 1.5-2 mm long; perianth c. 2.3 mm long, thinly pubescent. Anthers c. 6. *Moluccas, at low altitude* ***H. decalvata***³⁸
- b. Pedicel generally longer; perianth c. 2.5-3.5 mm long. *New Guinea, at c. 450-2000 m alt. Vegetatively and sometimes in fruit much resembling H. laevigata*³⁵ 38
- 38a. Male pedicel stoutish, 2-4 mm long. Male perianth \pm membranous, glabrescent, with or without a few scattered blackish warts. Anthers c. 8-12 ***H. corrugata***⁴⁰
- b. Male pedicel stout or rather slender, 2-5 mm long. Male perianth \pm fleshy, pubescent, without blackish warts. Anthers 5-10 ***H. pachycarpa***⁴¹
- 39a. Inflorescence moderately pubescent to nearly glabrous. Tomentum on leaf buds and apical portions of twigs short, rusty or greyish, the hairs 0.1-0.4(-0.5) mm long. Leaf largely or entirely (early) glabrescent, or with scattered stellate hairs beneath especially the younger ones 40
- b. Inflorescence generally thick-woolly tomentose. Tomentum on leaf bud and apical portion of twig usually rust-coloured, conspicuous, its hairs coarse and long, (0.3-) 0.5-1.5 mm. Leaves with (sub) persistent tomentum, at least on and near the midrib beneath 45
- 40a. Male perianth largely glabrous, subglobose, 2-3 mm diam., at anthesis cleft to the base, not collapsing on drying ***H. basifissa***³⁷
- b. Male perianth glabrous or hairy, of various sizes and shapes, at anthesis cleft to c. 1/2-way to near the base; perianth collapsing on drying or not 41
- 41a. Male perianth wholly or almost wholly clothed with \pm persistent tomentum, the hairs may be scattered and very minute. Leaves drying olivaceous to brown, without a reddish tinge; marginal nerve not conspicuously regularly looped. Hairs of leaf bud c. 0.1-0.2 mm long, usually greyish. *Moluccas, New Guinea, New Britain; not in the Solomon Isls.* 42
- b. Male perianth either glabrous, or early or late glabrescent, at least the upper 4/5. *E. New Guinea to Solomon Isl.* 43
- 42a. Mature male perianth small, c. 1.2-1.9 mm diam. *A variable species* ***H. pilifera***³⁶
- b. Mature male perianth 2.0-3.3 mm diam. *A variable species* ... ***H. laevigata***³⁵
- 43a. Perianths and pedicels glabrous; male perianth c. (20-) 2.5-3.5 (-4.0) mm diam. Leaves rather large, 20-40 cm long, drying olivaceous to brown, the

- marginal nerve rather indistinct and not very regularly looped. *Bagabag Isls., Long Isl., New Britain, New Ireland* **H. psilantha**³³
- b. Perianths and pedicels glabrous or pubescent; male perianth (1.0-) 1.5-2.0 (2.5 mm diam., see note 5 under *H. sinclairii*). Leaves drying generally with a reddish tinge, especially the midrib and nerves 44
- 44a. Leaves usually large, 9-30 (-40) cm long, the marginal nerve very distinct and conspicuously regularly looped. Hairs on leaf bud 0.1-0.4 mm, average c. 0.3 mm long, usually reddish brown, sometimes greyish. Pedicel and base of perianth minutely pubescent. Male perianth c. 1.5-2.0 mm diam., cleft at anthesis to c. 9/10. *Solomon Isl.* **H. whitmorei**³⁴
- b. Leaves smaller, 6-20 cm long, the marginal nerve indistinct and not very regularly looped. Hairs of leaf bud to c. 0.1 mm long, greyish brown. Pedicel and perianth glabrous (but see the notes). Male perianth c. 1.1-2.0 mm diam., at anthesis cleft to c. 1/2-way; perianth larger and pedicel pubescent in deviating specimens as discussed in note 5. *E. New Guinea* **H. sinclairii**³²
- 45a. Perianth in the male largely pubescent, towards the base thick-walled and coriaceous, the remainder collapsing on drying; both ♂ and ♀ opening at apex by small pore-like slit less than 1 mm long. Androecium subellipsoid, mainly consisting of the column with 2 minute anthers situated at the top, just below the pore. Leaves usually coriaceous, ± bullate; clothed with harsh hairs which when shed leave rough thickened bases. **H. pulverulenta**⁴²
- b. Perianth glabrous or pubescent, membranous or chartaceous, not much collapsing on drying, opening by a slit to at least c. 1/3. Androecium mainly consisting of 10-16 sessile anthers. Hairs on lower leaf surface not harsh, when shed not leaving rough thickened bases 46
- 46a. Perianth pubescent, in male at anthesis cleft to c. 3/4-5/6. Anthers 10-14. Leaves chartaceous or membranous **H. leptantha**⁴³
- b. Perianth glabrous, except at the very base; at anthesis cleft to c. 1/2-way or less. Leaves generally membranous 47
- 47a. Male perianth subglobose. Anthers 12-16. Leaves generally oblong to oblong-lanceolate, at apex not-caudate (always?) **H. hellwigii**⁴⁴
- b. Male perianth obovoid or ellipsoid. Anthers c. 10(-12). Leaves generally oblong-lanceolate, at apex caudate **H. ralunensis**⁴⁵
- 48a. Phyllotaxis in plagiotropic shoots (i.e. usually the fertile) dispersed, i.e., leaves in 3 or more rows along the twigs. Terminal leaf bud generally rather short and broad 49
- b. Leaves in plagiotropic shoots distichous (alternate), in rare cases, a few on the same plant in 3 rows. Terminal leaf bud generally more slender 57
- 49a. Leaves bunched towards the end of the twigs. Leaf bud and inflorescence pubescent with hairs c. 0.5-1.0 mm long. Bark of older twigs often blackish and flaking. *Borneo* **H. sabulosa**⁴⁶
- b. Leaves bunched or not. Tomentum on leaf bud and inflorescence short, the hairs up to c. 0.2 mm long, or, if plant from *Continental Asia*, then hairs short or long, up to c. 1 mm. Bark of older twigs flaking slightly or not 50
- 50a. Lower leaf surface with scattered brown to blackish non-traumatic dots (lens!) 51

- b. Lower leaf surface without dots 52
- 51a. Bark of twigs generally drying brown or grey-brown, not contrasting with the dark colour of the dried petioles; older bark not flaking. Leaves in 2 or 3 rows **H. glabra**¹⁰⁰
- b. Bark rather pale, grey-brown to pale yellowish-brown, rather contrasting with the petioles; older bark \pm flaking. Leaves in 3-5 rows. *Aceh (N. Sumatra)* at c. 1300 m **H. atjehensis**⁴⁷
- 52a. Bark of twigs drying brown, not contrasting with the colour of the dried petioles 53
- b. Bark of twigs drying pale, greyish-white or straw, contrasting rather well with the blackish brown colour of the dried petioles 55
- 53a. Twigs distinctly ridged or short-winged. *Sumatra* **H. hirtiflora**⁷¹
- b. Twigs terete, neither ridged nor winged 54
- 54a. Leaf pubescent beneath. *Sumatra, Malaya* **H. superba**⁵⁴
- b. Leaf glabrous beneath. *Borneo* **H. fragillima**⁸⁶
- 55a. Male pedicels at base articulated. Androecium much depressed, with the apical cavity conspicuous, broad, either shallow or rather deep, reaching up to nearly 1/2-way the androecium and bottom flattish; androphore narrow, largely hidden by the anthers. The leaves in most specimens distichous, sometimes 3-stichous). *Malaya, Sumatra* **H. sucosa** subsp. **sucosa**⁴⁸
- b. Male pedicels all or mostly not articulated. Androecium not or but slightly depressed, the apical cavity usually narrow and inconspicuous. Leaves generally in 3-5 rows 56
- 56a. Androphore indistinct or absent. Leaves generally drying blackish-brown. *Borneo* **H. pallidicaula**⁴⁹
- b. Androphore relatively distinct, 0.3-0.4 mm long. Leaves generally drying bright brown. *Sumatra, Malaya, penins. Thailand* **H. sparsa**⁵⁰
- 57a. Male perianth \pm obconical-obovoid, very leathery, at anthesis opening for 1/6-1/5 only. Androecium turbinate, anthers 3. *Sumatra* **H. triandra**⁵¹
- b. Male perianth of various shapes, opening for c. 1/5 or more. Androecium various, anthers 4 or more 58
- 58a. Mature male perianth in bud ellipsoid or obovoid, 3-8 mm long, at anthesis splitting c. 1/5-1/4 (-1/3). Leaves usually \pm parchment-like, on drying matt above owing to the finely wrinkled surface (in *H. sessilifolia* male flowers not known and leaves not so distinctly matt) 59
- b. Mature male perianth in bud either (1) ellipsoid or short-pear-shaped, c. 3.5 mm long or less (though sometimes rather large in *H. endertii*, *H. flocculosa*, *H. majuscula*, *H. wallichii*), or (2) perianth somewhat globose or depressed globose; perianth at anthesis cleft to (1/4-) 1/3-1/2, or more. Texture of leaves various including coriaceous, but never parchment-like and leaves not typically matt above 62
- 59a. Plant stout: twigs towards apex 5-7 (-10) mm diam.; leaves 25-70 cm long, tomentum present and persistent beneath 61

- b. Twigs towards apex 3-5 mm diam. Leaves up to 30 cm long, (largely) glabrous beneath, or with some hairs persisting on the midrib. Male perianth 3.0-5.0 mm long 60
- 60a. Leaves drying dark olivaceous; up to 32 cm long. Bark of twigs bright brown or yellowish-brown, coarsely striate and tending to crack longitudinally. Inflorescence (almost) glabrous. Pedicel not articulated. Anthers 12-20 **H. tristis**⁵²
- b. Leaves drying fulvous-brown; up to 24 cm long. Bark of twigs brown, finely striate, not cracking. Inflorescence pubescent. Pedicel articulated at base. Anthers 10-12 **H. fulva**⁵³
- 61a. Male perianth 7-8 mm long, perianth and pedicel glabrous. Petiole 6-15 mm long. *Malaya, Sumatra* **H. superba**⁵⁴
- b. Male flower not known; female perianth and pedicel pubescent. Petiole almost absent. *Borneo (Sarawak)* **H. sessilifolia**⁵⁵
- 62a. Leaves with a persistent or subpersistent tomentum below, in *H. gracilis* and *H. wallichii* the tomentum sometimes vestigial on and near midrib and nerves 63
- b. Leaves either glabrous or early glabrescent beneath, or in some species often with a vestigial pubescence on the lower midrib 74
- 63a. Leaf venation reticulate or not, not scabrous above 64
- b. Venation distinctly reticulate on both surfaces, older leaves scabrous above **H. grandis**⁵⁶
- 64a. Leaves with scattered dark brown or blackish dots and/or streaks beneath, obscured by hairs or not 65
- b. Leaves without dots or streaks beneath 66
- 65a. Mature male perianth in bud short-pear-shaped, c. 2-2.5 mm long; pedicel indistinct, c. 0.3-1.0 mm long. Leaves rather thinly pubescent, often \pm glabrescent beneath **H. wallichii**⁵⁷
- b. Mature male perianth subglobose, c. 1-1.5 mm diam., pedicel distinct, c. 1-1.5 mm long. Leaves with persistent, conspicuous tomentum beneath **H. pulcherrima**⁵⁸
- 66a. Mature male perianth in bud broadly ellipsoid or obovoid, 2-3 mm long; androecium longer than broad. Pedicel (1.5-) 3-4 mm long. Tomentum on twigs and lower leaf surface with hairs c. 1.5-2 mm long **H. flocculosa**⁵⁹
- b. Mature male perianth subglobose or depressed globose, c. 2.5 mm diam. or less; androecium as broad as or broader than long. Pedicel 3 mm long or less. Tomentum on twigs and lower leaf surface with hairs to c. 1.5 mm long 67
- 67a. Male perianth to c. 1 mm diam., with persistent tomentum or late glabrescent **H. motleyi**⁶⁰
- b. Male perianth c. 1.0-2.5 mm diam., glabrous or early glabrescent 68
- 68a. Male pedicel at base not articulated (character not quite clear in *H. rufo-lanata*; male flower not seen in *H. gracilis*) 69
- b. Male pedicel with distinct articulation at base 73

- 69a. Upper leaf surface drying dark brown, with the venation (reticulation) usually indistinct. *Malaya, S. penins. Thailand* **H. tomentosa**⁶
- b. Leaves drying olivaceous to brown, with the reticulation on upper surface distinct or not. *Borneo* 70
- 70a. Twigs stoutish, diam. towards the apex 3.5-7 (-13) mm. Leaves 10-45 cm long. Tertiary venation usually distinct above. Lateral nerves c. 11 pairs or more. Male perianth c. 1.5-2.3 mm diam.; anthers 8 or more. *Plant growing generally on soils richer than kerangas or sand* 72
- b. Twigs slender, diam. towards the apex up to c. 3 mm. Leaves small, c. 7-21 cm long. Tertiary venation usually indistinct above 71
- 71a. Twigs 1.5-2.5 mm diam. Leaves thinly membranous, 12-21 cm long; lateral nerves 14-17 pairs. Lower leaf surface with tomentum rather sparse, subpersistent, the hairs vestigial mainly on nerves and midrib. Male flower not seen. *Primary lowland forest* **H. gracilis**⁶²
- b. Twigs c. 2-3 mm diam. Leaves 7-15 cm long, \pm chartaceous; lateral nerves 5-9 pairs. Lower leaf-surface with denser tomentum. Male perianth c. 1.0 mm diam.; anthers 4 or 5. *Kerangas forest, or forest on coastal white sand* **H. paucinervis**⁶³
- 72a. Leaves generally large, 18-45 cm long; lateral nerves 18-25 pairs, sunken in upper surface. Male perianth c. 1.5-2.0 mm diam., anthers 8-10 **H. splendida**⁶⁴
- b. Leaves smaller, 10-23 cm long; lateral nerves 11-16 pairs, raised above. Male perianth c. 2-2.3 mm diam.; anthers c. 15. *A montane species at c. 900-1400 m alt. in Sarawak, Sabah* **H. rufo-lanata**⁶⁵
- 73a. Leaves membranous, not bullate; veins in upper surface flat or sunken, reticulation rather faint to distinct. Male perianth 1.5-2.2 mm diam.; pedicel equal to or somewhat longer than the perianth **H. affinis**⁶⁶
- b. Leaves chartaceous, bullate; veins sunken, reticulation very distinct. Male perianth 2-2.5 mm diam.; pedicel as long as or shorter than the perianth **H. reticulata**⁶⁷
- 74a. Twigs in apical portion pale, grey-whitish or pale straw coloured, contrasting with the blackish or dark brown colour of the dried petiole 75
- b. Twigs in apical portion drying brown to dark grey-brown, not contrasting with the brown to blackish colour of the dried petiole 78
- 75a. Androecium in transverse section triangular. Anthers mutually free for the upper half of more. *Borneo: heath forest on sand or peat soil* **H. oligocarpa**⁸²
- b. Androecium in transverse section circular or subcircular. Anthers largely connate 76
- 76a. Leaves chartaceous, drying bright brown. Pedicel at base not articulate. Androecium with small apical cavity. *Borneo: mostly in heath forest or kerangas forest on sandy soils* **H. carnosa**⁶⁹
- b. Leaves membranous, drying usually \pm brown or blackish brown. *Plant growing usually in forest on richer soils, incl. sand.* 77
- 77a. Pedicel articulated at base. Androecium strongly-depressed globose, with the apical cavity broad and the bottom flattish, cavity nearly 1/2-way deep.

- Malaya, Sumatra* **H. sucosa** subsp. *sucosa*⁴⁸
- b. Pedicel not articulated at base. Androecium ellipsoid to slightly depressed globose, the apical cavity small and narrow. *Borneo* **H. pallidicaula**⁴⁹
- 78a. Twigs distinctly ridged or nearly winged in between the petiole insertions, also in the older wood 79
- b. Twigs not ridged; sometimes twigs faintly ridged, or lined or angular in the apical portion only 82
- 79a. Male perianth at anthesis cleft nearly to the base. *New Guinea* 80
- b. Male perianth at anthesis cleft to c. 1/2-2/3. *West Malesia* 81
- 80a. Male perianth slightly broader than long, short-pubescent in the lower half. Androecium slightly broader than long; anthers erect, not incurved **H. angularis**²⁶
- b. Male perianth subglobose to broadly ellipsoid, glabrous. Androecium longer than broad, \pm obovoid, the anthers with apex free and incurved, those of one side of the androecium clasping the others **H. olens**¹⁷
- 81a. Mature male perianth in bud c. 2.5 mm diam., pubescent. *N. Sumatra* **H. hirtiflora**⁷¹
- b. Mature male perianth in bud c. 1.0-1.5 mm diam., glabrous. *S. penins. Thailand, Malaya, Sumatra, Borneo* **H. brachiata**⁷²
- 82a. Mature male perianth in bud short-pear-shaped, c. 2.0 (-2.5) mm long, subsessile; the pedicel much shorter than the perianth, c. 0.3-1.0 mm long, thickish. Leaves coriaceous; lateral nerves flat or usually sunken above, pubescent or glabrescent beneath and with scattered blackish dots and streaks (lens!). Twigs towards the apex usually conspicuously hollow **H. wallichii**⁵⁷
- b. Male perianth various in shape and size, the pedicel proportionally longer and more slender; perianth obovoid with pedicel short in *H. glabra* var. *oviflora*. Leaves various, nerves raised or sunken, dotted or not beneath. Twigs solid or generally less strikingly hollow 83
- 83a. Male inflorescence very stout, the rachis towards the base 5-8 mm diam. Androecium about as broad as long, triquetrous, the anthers entirely connate. *W. Borneo* **H. pachyrachis**⁷³
- b. Male inflorescence large or small, the rachis towards base c. 4.0 (-4.5) mm thick or less. Androecium of various shape, in transverse section triquetrous or circular. *Whole of W. Malesia* 84
- 84a. Androecium in transverse section 3- or 4-angular. Anthers \pm erect, for a large part mutually free, usually for c. 1/2-way or more. Lateral nerves raised above, except in *H. ridleyana* (with leaves small, and male perianth c. 1 mm diam.). Leaves not dotted beneath. Male perianth c. 1.5 (-2.0) mm diam. or less. Pedicel articulated at base. *Most of W. Malesia, not in Celebes, rare in the Philippines* 85
- b. Androecium in transverse section either circular or \pm ellipsoid, or sub-triangular with rounded angles, neither triquetrous nor quadrangular. Anthers \pm curved, almost entirely connate; free apices c. 1/3 or less. Leaf, with the lateral nerves raised above, or level, or sunken; with or without blackish dots (lens!) beneath, the dots not to be confused with a much finer punctation present or not. Male perianth c. (1.3-) 1.5 mm diam. or more.

- Pedicle at base articulated or not 92
- 85a. Leaves small, 5-16 cm long. Lateral nerves \pm level or sunken above; midrib either little raised, or flat, or sunken 86
- b. Leaves small or large, 5-28 cm long. Midrib and lateral nerves raised above 87
- 86a. Anthers 4-6. Nerves above usually indistinct or invisible. Leaf apex acute or acute-acuminate. Twigs at apex and inflorescence rather glabrescent. *Malaya, Borneo* **H. ridleyana**⁷⁴
- b. Anthers 9 or 10. Nerves flat or but little raised above, well visible. Leaf apex blunt. Twig apex rather late glabrescent, inflorescence with persistent tomentum. *Sarawak* **H. obtusa**⁷⁵
- 87a. Flower not seen. Leaves early glabrescent, also on the midrib; leaf apex long acute-acuminate. Bark of twigs rather smooth, lower down cracking longitudinally. *Brunei* **H. disticha**⁷⁶
- b. Leaves early glabrescent, the midrib beneath early or later glabrescent; leaf apex acute-acuminate. Bark of twigs striate, lower down coarsely striate or finely cracking 88
- 88a. Twigs slender, towards apex 1-2 (-4) mm diam. Leaves rather small, 7-18 cm long, thinly membranous to subchartaceous; petiole slender, diam. 1-1.5 (-2.0) mm. Male inflorescence delicate, up to 9 cm long. Mature male perianth small, diam. c. 1.0 mm 89
- b. Twigs towards apex 1-5 (-8) mm diam. Leaves of various size, chartaceous to coriaceous; petiole 1.5-4 (-8) mm diam. Male inflorescence up to 15(-20) cm long. Male perianth 1.0-2.0 mm diam 90
- 89a. Leaf bud with tomentum composed of hairs c. (0.1-) 0.2 mm long; twigs at apex and leaves glabrous; inflorescence with rather sparse tomentum of stellate hairs c. 0.2 mm long, glabrescent. Leaves drying to a greyish tinge. Mature male perianth in bud rather short-pear-shaped, shortly tapering into the pedicel **H. tenuifolia**⁷⁷
- b. Leaf bud, apical portion of twig, petiole and inflorescence with woolly tomentum of stellate-dendroid hairs c. (0.2-) 0.5 mm long; leaves with rather persisting hairs on midrib beneath, drying olivaceous. Mature male perianth in bud globose or depressed-globose **H. macilenta**⁷⁸
- 90a. Plant robust, twigs stout, leaves coarse, the midrib broad above, at the transition to the petiole at least 3 mm wide. Male inflorescence 10-20 cm long. *Borneo: forests on poor soil, including sand and peat* **H. laticostata**⁷⁹
- b. Plant generally less robust; leaves various, the midrib above towards the insertion of the petiole less than 3 mm wide. Male inflorescence up to 15 cm long. *Forests, on poor or rich soil* 91
- 91a. Leaves 16-28 cm long; nerves 16-19 pairs, very prominent above; leaf base \pm rounded or short-attenuate. *Borneo: Sarawak* **H. nervosa**⁸⁰
- b. Leaves 7-28 cm long, base short- to long-attenuate; nerves 6-16 pairs, raised to various degree above. On drying, colour of leaves above and below usually much contrasting, generally more so than in the related species. (A variable species, especially the fruits.) *Malaya, Sumatra, whole of Borneo, Philippines (Mindanao)* **H. polyspherula**⁸¹

- 92a. Leaf bud, apical portion of twig, and inflorescence with tomentum of hairs c. 0.2 mm long or more; hairs 0.1-0.4 mm long in *H. punctata* 93
- b. Leaf bud, apical portion of twig, and inflorescence with tomentum of hairs less than 0.2 mm long; hairs usually c. 0.1 mm long or less 100
- 93a. Mature male perianth in bud ellipsoid, c. 2.5-3.5 mm long; androecium longer than broad. Leaves generally drying thick and brittle, tip bluntish. Lower leaf surface usually with conspicuous pale golden hair scars (lens!) ...
..... **H. endertii**⁸³
- b. Mature male perianth globose or subglobose; androecium not longer than broad 94
- 94a. Mature male perianth in bud c. 2.5-3.0 mm diam. (or c. 1.5 mm in a deviating specimen *Hallier 624* from *W. Borneo*, see the notes), at anthesis cleft to c. 4/5. *Sumatra* **H. valida**⁸⁴
- b. Mature male perianth in bud c. (1.0-) 1.2-2.5 mm diam., at anthesis cleft to 1/3-2/3 (-3/4). *Malaya, Borneo* 95
- 95a. Pedicel in male flowers not articulated at the base. Leaves without blackish dots or streaks below (lens!). Lateral nerves largely raised above. On drying, colour of upper and lower leaf surface not much contrasting 96
- b. Pedicel at base articulated. Leaves with scattered blackish brown dots and stripes beneath. Lateral nerves above largely flat or sunken, rarely faintly or partially raised. Upper leaf surface drying greenish or blackish brown, usually rather contrasting in colour with the cinnamon- or chocolate-coloured lower surface **H. borneensis**⁸⁵
- 96a. Male perianth c. 2.0-2.5 mm diam. Androecium sessile, \pm saucer-shaped and broadly hollow. Leaves 20-45 cm long. *Lowland forest*
..... **H. fragillima**⁸⁶
- b. Male perianth c. (1.0-) 1.4-2.2 mm diam. Androecium \pm globose or depressed-globose, with the apical cavity small, concealed by the overhanging anther tips. Leaves 4-35 cm long. *Montane forest at 800-200 m* 97
- 97a. Androecium borne by a distinct slender androphore c. 0.3-0.8 mm long, not hidden by the anthers. Leaves membranous, 9-18 cm long, drying dark brown, leaf tip acute-acuminate **H. androphora**⁸⁷
- b. Androecium sessile, with the androphore absent or short, up to 0.5 mm, largely or completely hidden by the anthers 98
- 98a. Leaves chartaceous or membranous, to c. 35 cm long, drying olivaceous to brown above; leaf tip acute-acuminate. Male inflorescence large, to c. 20 cm long. *Borneo* **H. amplomontana**⁸⁸
- b. Leaves coriaceous, 4-14 cm long, drying olivaceous brown or blackish above; leaf tip obtuse to subacute. Male inflorescence 4-16 cm long 99
- 99a. Leaves drying dark brown to blackish, lower surface not punctate. *Borneo*
..... **H. montana**⁸⁹
- b. Leaves drying olivaceous brown, lower surface densely brown-black punctate (lens!). *Malaya* **H. punctata**⁹⁰
- 100a. Leaves dotted or coarsely punctate beneath; dots brown to blackish, or rarely pale brown, \pm regularly spaced and equal-sized, of non-traumatic origin 107

- b. Leaves not dotted beneath (dotting should not be confused with generally smaller, irregularly spaced, blackish mottles or points, or with dots of various sizes of traumatic origin) 101
- 101a. Male perianth \pm ellipsoid; androecium \pm obovoid, the anthers with their apical portions deeply inflexed into a deep apical cavity. *New Guinea* *H. sepikensis*¹⁸
- b. Male perianth and androecium of various shapes; the anthers \pm straight or curved, at apex not inflexed. *W. and E. Malesia, not in New Guinea* 102
- 102a. Male perianth coriaceous; valves thick, towards the base (0.3-) 0.4-1.0 mm thick. Androecium ellipsoid-obovoid, longer than broad 105
- b. Male perianth thinner, valves at base c. 0.2-0.3 mm thick. Androecium subglobose or broadly ellipsoid or broadly obovoid, not or but little longer than broad. Androphore narrow, and only c. 0.2 mm long. Leaves membranous to chartaceous 103
- 103a. Male pedicel (1-) 1.5-2 mm long, about as long as the perianth. *Malaya, Borneo* 104
- b. Male pedicel shorter than the perianth, c. 0.5 mm long. *Celebes, Philippines* *H. costulata*⁹¹
- 104a. Male perianth at anthesis cleft to c. 1/2-way *H. subalpina*⁹²
- b. Male perianth at anthesis cleft to c. 2/3-4/5 *H. obscura*⁹³
- 105a. Bark of twigs not flaking. Leaves membranous 106
- b. Bark of twigs flaking or not. Leaves coriaceous. Male pedicel at base not articulated. Anthers 5-8. Androphore rather broad, tapering, (0.1-) 0.2-0.3 mm long. *Kerangas forest, mountain forest; 800-1200 m alt.; Sarawak, Sabah* *H. xanthina*⁹⁴
- 106a. Pedicel of male flowers articulate at base. Anthers 7-9. Androphore rather broad and tapering, 0.2-0.5 mm long. *Forest, 0-1000 m; Malaya; Sumatra* *H. majuscula*⁹⁵
- b. Pedicel at base not articulated. Anthers 5 or 6. Androphore narrow, 0.1-0.2 mm long, hidden by the anthers. *Forest, c. 100-450 m; C. Celebes* *H. coriacea*⁹⁶
- 107a. Twigs moderately stout, towards the apex c. 2.5-3 (-4) mm diam. Leaves (8-) 12 cm long or more. Male perianth globose or subglobose, diam. c. 1.5-4.2 mm 108
- b. Twigs slender, diam. towards the apex 1.5-2.0 mm. Leaves c. 5-12 cm long. Perianth \pm ellipsoid to globose, 1.2-1.8 mm long *H. penangiana*⁹⁷
- 108a. Male perianth at anthesis cleft to c. 3/4-4/5. Anthers 7-11 109
- b. Male perianth at anthesis cleft to c. 1/3-2/3. Anthers 9-20. *Sumatra, Java* 110
- 109a. Anthers 7-9. Dry fruits c. 4-5 cm long, pericarp 10-20 mm thick. *N. Sumatra, Malaya, Borneo* *H. punctatifolia*⁹⁸
- b. Anthers c. 11. Dry fruits c. 2 cm long, pericarp c. 1.5 mm thick. *Malaya* *H. punctata*⁹⁹

- 110a. Male perianth 3.0-4.2 mm diam.; anthers 15-20 **H. macrothyrsa**⁹⁹
 b. Male perianth c. 1.5-2.5 mm diam.; anthers 9-15. *A variable species with 3 varieties* **H. glabra**¹⁰⁰

(2-7) REGIONAL KEYS TO THE SPECIES FOR FEMALE FLOWERING
 AND FRUITING SPECIMENS

based partly on vegetative characters and distribution

(2) CEYLON, CONTINENTAL SE. ASIA (INCL. PENINSULAR THAILAND, EXCL. MALAYSIA
 AND SINGAPORE), AND ANDAMAN SL.

- 1a. Ovary pubescent. Fruit pubescent at least at the base, or in *H. kingii* glabrescent 2
 b. Ovary glabrous. Fruit glabrous 4
 2a. Female perianth pubescent at least at the base. Leaves glabrous or late-glabrescent below, or with vestigial tomentum on the midrib. Fruit c. 2.5 cm long or more 3
 b. Perianth glabrous. Leaves with persistent tomentum below. Fruit c. 1.5-2.0 cm long, glabrescent but with vestigial tomentum towards the base; perianth not persisting. *S. penins. Thailand* **H. tomentosa**⁶¹
 3a. Perianth pubescent at base. Fruit ellipsoid, c. 2.5-4 cm long, wholly pubescent; perianth not persisting. *Ceylon* **H. iryagedhi**¹
 b. Perianth wholly pubescent, or partly glabrescent. Fruit \pm ellipsoid-oblong, (3-) 4-6 cm long, glabrescent, with the perianth persisting. *NE. India to S. China* **H. kingii**²
 4a. Twigs towards apex either subterete, or usually \pm flattened or angular, and lined or ridged from petiole to petiole. Phyllotaxis distichous 5
 b. Twigs terete, not lined. Leaves distichous or in 3-5 rows along the twigs. Fruit ellipsoid 6
 5a. Twigs lined. Perianth 2-valved. Leaves often with irregularly shaped whitish marks or blotches here and there. Fruit globose, c. 1.5-2.0 cm diam., pericarp 1-2 mm thick; seed globose. *Plant usually growing not too far from the coast* **H. irya**⁶
 b. Twigs more prominently lined or ridged, usually distinctly angular in section. Leaves without whitish marks. Fruit ellipsoid, c. 2.0-3.0 cm long, pericarp 1.5-4 mm thick; seed ellipsoid. *Not coastal penins. Thailand* **H. brachiata**⁷²
 6a. Bark of twigs drying pale, grey-brown, contrasting with the blackish colour of the dried petiole. Fruit drying blackish, c. 3.0-5.5 cm long; pericarp c. 5-15 mm thick. Perianth 3- (or 4-) valved. *Penins. Thailand* **H. sparsa**⁵⁰
 b. Twigs drying brown, not much contrasting with the petiole. Fruit usually (dark) brown, c. 1.5-3.5 cm long; pericarp c. 1-2.5 mm thick. Perianth 2- or 3-valved 7
 7a. Fruit c. 1.5 cm long. Leaves distichous. *C. Vietnam (Annam)* **H. longiflora**³
 b. Fruit generally larger, c. 1.8-3.4 cm long. Leaves distichous or dispersed .. 8
 8a. Leaves in 3-5 rows along the twigs. Tomentum of leaf bud composed of hairs c. 0.1-0.3 mm long. Male perianth c. 1.0-1.5 mm diam. *Indo-China*

..... **H. thorelii**⁴

- b. Leaves either distichous or dispersed in 3 or 5 rows. Tomentum of leaf bud composed of hairs either c. 0.1 mm long or c. 0.5-1.0 mm long. Male perianth c. 1.5-2.3 mm diam. *NE. India, S. China (Yunnan), Indo-China, Andaman Isl.* **H. amygdalina**⁵

(3) MALAYA, SINGAPORE

- 1a. Female perianth at base pubescent; ovary and fruit pubescent. Fruit ellipsoid, c. 2.5-4 cm long. Flowers in dense clusters and strongly fragrant in male specimens. *Originating from Ceylon, cultivated in Penang, Singapore* **H. iryagedhi**⁷
- b. Perianth glabrous 2
- 2a. Perianth 2-valved. Ovary glabrous 3
- b. Perianth 3- (or 4-) valved. Ovary glabrous or pubescent 5
- 3a. Twigs usually shallowly ridged or lined from petiole to petiole. Leaves membranous, often with irregularly shaped whitish marks or blotches here and there. Fruit globose, c. 1.5-2.0 cm diam., glabrous; pericarp 1-2 mm thick; seed globose. *Plant usually growing not too far from the coast* **H. irya**⁶
- b. Twigs not lined. Leaves without pale blotches. Fruit and seed ellipsoid 4
- 4a. Leaves membranous, glabrous beneath, not brown dotted. *Gardens' Jungle, Singapore* **H. parviflora**¹⁰
- b. Leaves coriaceous, pubescent below and with regularly spaced, small, brown to blackish dots (lens!). *Kerangas forest, peat swamp forest* **H. crassifolia**⁶⁸
- 5a. Leaves on lower surface with \pm regularly spaced, dark brown or blackish dots being cork warts originating from hair scars; dots not to be confused with usually smaller dark punctation of different origin, present or not (lens!) 19
- b. Leaves not dotted beneath 6
- 6a. Leaves with persistent tomentum beneath 7
- b. Leaves glabrous or glabrescent beneath 11
- 7a. Ovary pubescent. Fruit pubescent or at least with vestigial tomentum near the base; perianth not persisting under the fruit **H. tomentosa**⁶¹
- b. Ovary glabrous or only with some incidental minute hairs. Fruit glabrous, the perianth (at least at first) persisting 8
- 8a. Hairs on lower (and upper) leaf surface harsh, with hardened hair-bases, in older leaves rendering the surface scabrous. Fruit c. 1.0-1.4 cm long **H. grandis**⁵⁶
- b. Leaves not scabrous. Fruit c. 2 cm or more long 9
- 9a. Twigs of moderate habit, towards the apex c. 3-5 mm diam. Tomentum of leaf bud and the very twig apex composed of hairs c. 0.2-0.3 mm long. Leaves drying dull above, 13-21 cm long. Fruit c. 2.2-2.4 (-3.0) cm long **H. fulva**⁵³

- b. Twigs stouter, diam. towards apex c. 5-10 mm. Tomentum with hairs c. 0.5 mm long or more. Leaves c. 20-40 (-70) cm long 10
- 10a. Tomentum of leaf bud, twig apex and lower leaf surface with hairs c. 0.5-1.0 mm long, rather stiff, rust-coloured. Fruit c. 3.8-5.5 cm long **H. superba**⁵⁴
- b. Tomentum composed of woolly hairs c. 1.0-2.0 mm long, yellow-brown or pale brown. Fruit c. 3 cm long **H. flocculosa**⁵⁹
- 11a. Bark of twigs drying rather pale, pale brown or yellowish brown, or straw, contrasting with the blackish colour of the dried petiole. Phyllotaxis either distichous, or the leaves in 3-5 rows along the twigs 12
- b. Twigs drying brown, the colour not considerably contrasting with the petiole. Leaves distichous 13
- 12a. Leaves distichous or in 3 rows. Fruit c. 2.5-3.5 cm long, with the perianth persisting. Pedicel articulated at base (this character best seen in male flowers) **H. sucosa** subsp. **sucosa**^{48a}
- b. Leaves in 3-5 rows along the twigs. Fruit c. 3-5.5 cm long, the perianth not persisting. Pedicel at base not articulated **H. sparsa**⁵⁰
- 13a. Leaves drying very dull above because of finely wrinkled surface; nerves flat or sunken. Fruit usually with persistent perianth **H. fulva**⁵³
- b. Leaves above not particularly dull, not finely wrinkled; nerves flat or raised. Perianth not persisting under the fruit 14
- 14a. Lateral nerves flat or but faintly raised above 15
- b. Lateral nerves on upper leaf surface distinctly raised. Pedicel at base articulated (this character best seen in male flowers) 16
- 15a. Tomentum of leaf bud composed of hairs c. 0.1 mm long. Twigs towards the apex c. 2.5-5 mm diam. Leaves 15-27 cm long. Pedicel at base not articulated **H. subalpina** subsp. **subalpina**^{92a}
- b. Tomentum of leaf bud with hairs c. 0.2-0.4 mm long. Twigs slender, towards the apex c. 1.5-3.5 mm diam. Leaves c. 5-15 cm long. Pedicel at base articulated **H. ridleyana**⁷⁴
- 16a. Tomentum of leaf bud composed of hairs c. 0.1 mm long. Midrib beneath early glabrescent. Fruit c. 4.5-6.5 cm long, usually with thick pericarp **H. majuscula**⁹⁵
- b. Tomentum of leaf bud with hairs c. 0.1 mm long or usually much longer. Midrib beneath often rather late glabrescent. Fruit c. 2-4 cm long, pericarp c. 2-5 (-7) mm thick 17
- 17a. Twigs \pm angular by lines or low ridges from petiole to petiole. Fruit c. 2-3 (-4.0) cm long **H. brachiata**⁷²
- b. Twigs terete, neither lined nor ridged 18
- 18a. Twigs towards the apex c. 2-5 mm diam. Leaves usually chartaceous. Fruit 1.9-3.5 cm long **H. polyspherula**⁸¹
- b. Twigs more delicate, towards the apex c. 1-3 mm diam. Leaves membranous. Fruit c. 2.3-2.4 cm long **H. macilentia**⁷⁸

- 19a. Leaves usually with persistent tomentum beneath 20
- b. Leaves glabrous or glabrescent beneath 21
- 20a. Lower leaf surface with small dots and dashes; pubescent, sometimes late glabrescent. Ovary glabrous. Fruit c. 4-6 cm long, glabrous, with the perianth usually persistent **H. wallichii**⁵⁷
- b. Lower leaf surface always pubescent, provided with only dots, not with streaks. Ovary pubescent. Fruit c. 1.6-1.8 cm long, shaggy-hairy, the perianth not persistent **H. pulcherrima**⁵⁸
- 21a. Twigs delicate, towards the apex c. 1.5-2 mm diam. Fruit c. 1.1-2.0 cm long **H. penangiana**⁹⁷
- b. Twigs somewhat stouter, diam. towards apex c. 2.5-5 mm. Fruit c. 2 cm long or more 22
- 22a. Leaves coriaceous, tip blunt or subacute. Fruit c. 2-2.3 cm long, pericarp thin. *A mountain species of central Malaya* **H. punctata**⁹⁰
- b. Leaves membranous, tip acute-acuminate. Fruit 4.5-8 cm long, pericarp 10-20 mm thick. *Forests up to c. 1100 m. alt.* **H. punctatifolia**⁹⁸

(4) SUMATRA, JAVA

- 1a. Female perianth at base pubescent; ovary pubescent. Fruit ellipsoid, c. 2.5-4 cm long, pubescent. *Male specimens with the flowers in dense clusters, strongly fragrant. Cultivated, originating from Ceylon* **H. iryagedhi**¹
- b. Perianth glabrous 2
- 2a. Leaves membranous, often with irregularly shaped whitish blotches here and there. Female perianth 2-valved; ovary glabrous. Fruit globose, c. 1.5-2.0 cm diam., glabrous; pericarp 1-2 mm thick; seed globose. *Plant usually growing not too far from the coast* **H. irya**⁶
- b. Leaves of various consistency, usually not white-blotched. Fruit ellipsoid; seed ellipsoid. *Plant coastal or not* 3
- 3a. Perianth 2-valved. Lower leaf surface with \pm regularly scattered brown to blackish dots, originating from hair scars; dots not to be confused with usually smaller punctation of different origin (lens!) 4
- b. Perianth 3-(or 4-) valved. Lower leaf surface dotted or not 5
- 4a. Leaves coriaceous, 10-20 (-28) cm long, finely pubescent on the lower surface. Twigs towards apex 2-6 mm diam. Fruit c. 1.5-2.2 cm long, with persistent perianth. *Peat swamp forest* **H. crassifolia**⁶⁸
- b. Leaves membranous or thinly chartaceous, 5-12 cm long, glabrous beneath. Twigs c. 1.5-2 mm diam. Fruits 1-2 cm long; perianth not persisting. *Mixed forest* **H. penangiana**⁹⁷
- 5a. Ovary and fruit (at least at base) pubescent. Lower leaf surface with persistent tomentum 6
- b. Ovary and fruit glabrous. Lower leaf surface glabrous or pubescent 7
- 6a. Twigs towards the apex c. 2-5 mm diam. Leaves c. 9-27 cm long, lower surface without dots. Fruit with hairs c. 0.5 mm long or less. *Thailand,*

- Malaya; specimens from Sumatra not seen* **H. tomentosa**⁶¹
- b. Twigs stouter, towards apex 5-8 mm diam. Leaves c. 20-36 cm long, lower surface with regularly scattered brown to blackish dots (lens!). Fruit with hairs c. 2 mm long **H. pulcherrima**⁵⁸
- 7a. Lower leaf surface with more or less regularly spaced brown to blackish dots (lens!). Lateral nerves in upper surface generally flat or sunken 21
- b. Lower leaf surface without dots. Nerves either raised, or flat to sunken ... 8
- 8a. Lower leaf surface with persistent tomentum. Fruit with persistent perianth 9
- b. Lower leaf surface glabrous or glabrescent. Fruit with perianth persistent or not 11
- 9a. Hairs harsh, the hair scars making the lower surface of older leaves scabrous. Fruit 1-1.4 cm long **H. grandis**⁵⁶
- b. Older leaves not scabrous beneath 10
- 10a. Plant stout, twigs towards apex c. 5-8 mm diam.; leaves c. 20-40 (-70) cm long. Tomentum of leaf bud with hairs c. 0.5-1.0 mm. Fruit 3.8-5.5 cm long **H. superba**⁵⁴
- b. Twigs towards the apex c. 3-5 mm diam.; leaves 13-21 cm long. Hairs on leaf bud c. 0.2-0.3 mm long. Fruit c. 2-3 cm long **H. fulva**⁵³
- 11a. Lateral nerves in upper leaf surface flat or sunken or but faintly raised. On drying, colour of lower leaf surface generally greyish brown, not contrasting with that of the upper surface 12
- b. Lateral nerves distinctly raised above. On drying, colour of the lower leaf surface bright brown or chocolate, usually much contrasting with the upper surface 16
- 12a. Twigs delicate, towards the apex c. 1.5-3 mm diam.; leaf bud, the very twig apex and young inflorescence woolly-pubescent with hairs c. 0.3-0.7 mm. Leaves 5-9 cm long. *Female flower and fruit not known* **H. triandra**⁵¹
- b. Twigs generally stouter, towards apex (2-) 3-10 mm diam.; hairs of leaf bud and inflorescence c. 0.1-0.3 mm long. Leaves more than 10 cm long 13
- 13a. Leaves distichous, drying dull because of minutely wrinkled upper surface. Bark of twigs straw-colour or brown 14
- b. Leaves distichous or arranged along the twigs in 3-5 rows; not particularly dull from drying, upper surface not finely wrinkled. Bark of twigs pale, grey-brown or straw, contrasting with the blackish colour of the dried petiole 15
- 14a. Leaves elliptic-oblong to oblong, drying olivaceous to brown above. Stem grey-brown, not conspicuously contrasting with the colour of the dried petiole. Fruit drying brown, c. 2.2-3 cm long, perianth persistent **H. fulva**⁵³
- b. Leaves elliptic-oblong to lanceolate, drying to a rather dark olivaceous colour above. Stem pale \pm yellowish-brown, rather contrasting with the petiole. Fruit drying blackish, c. 1.5 cm long, the perianth not persisting **H. tristis**⁵²

- 15a. Leaves distichous or in 3 rows. Fruit c. 2.5-3.5 cm long, with the perianth persisting. Pedicel articulated at base (this character best seen in male flowers) **H. sucosa** subsp. *sucosa*^{48a}
- b. Leaves in 3-5 rows along the twigs. Fruit c. 3-5.5 cm long, the perianth not persisting. Pedicel at base not articulated **H. sparsa**⁵⁰
- 16a. Perianth 4-valved. Pedicel at base not articulate (this character best seen in male flowers). (Female perianth known only from the remnants persisting under young fruits). Fruit c. 8-9 cm long **H. valida**⁸⁴
- b. Perianth generally 3-valved. Pedicel articulate at base. Fruit up to 6.5 cm long 17
- 17a. Twigs angular or subterete, provided with lines or ridges from petiole to petiole 18
- b. Twigs terete or but faintly angular, neither lined nor ridged 19
- 18a. Perianth pubescent (known only from male flowers). Fruit c. 5-6 cm long. *N. Sumatra* **H. hirtiflora**⁷¹
- b. Perianth glabrous. Fruit c. 2-4 cm long **H. brachiata**⁷²
- 19a. Twigs delicate, towards the apex c. 1-3 mm diam. Leaves membranous, midrib beneath late-glabrescent. Fruit c. 2.3-2.4 cm long **H. macilenta**⁷⁹
- b. Twigs generally stouter, towards the apex c. 2-5 mm diam. Leaves usually chartaceous. Fruit 1.9-6.5 cm long 20
- 20a. Tomentum of leaf bud and inflorescence composed of hairs c. 0.1-0.2 mm long. Midrib beneath early glabrescent. Fruit c. 4.5-6.5 cm long **H. majuscula**⁹⁵
- b. Tomentum with hairs 0.1-0.6 mm long. Midrib often late-glabrescent. Fruit 1.9-3.5 cm long. *A variable species* **H. polyspherula**⁹¹
- 21a. Lower leaf surface usually with persistent tomentum (sometimes glabrescent), and with small scattered dots and streaks (lens!). Twigs conspicuously hollow. Fruit c. 4-6 cm long, the perianth generally persistent **H. wallichii**⁵⁷
- b. Leaves beneath glabrous or glabrescent; dotted, not streaked. Twigs not conspicuously hollow. Fruit various 22
- 22a. Bark of twigs pale, greyish to straw, much contrasting with the blackish colour of dried petiole. Phyllotaxis dispersed, with the leaves in 3-5 rows. *Female flower and fruit not known. N. Aceh, at c. 1300 m* **H. atjehensis**⁴⁷
- b. Bark of twigs brown, not contrasting in colour with the petiole. Leaves distichous, or in 3 rows in *H. glabra*, *p.p.* 23
- 23a. Fruit large, (4.5-) 5-8 cm long, with thick pericarp **H. punctatifolia**⁹⁹
- b. Fruit c. 1-2.5 cm long, pericarp much thinner 24
- 24a. Twigs slender, diam. towards the apex c. 1.5-2 mm. Leaves 5-12 cm long. Fruit c. 1.1-2.0 cm long **H. penangiana**⁹⁷
- b. Twigs generally stouter, towards apex c. 2.5-4 (-6) mm diam. Leaves (8-) 12 cm long or more. Fruit c. 1.8-2.5 cm long 25

- 25a. Leaves distichous. *C. & N. Sumatra* **H. macrothyrsa**⁹⁹
 b. Leaves distichous or dispersed in 3 rows. *Java, S. Sumatra, Mentawai
 Isls. north to Simeuluë Isl.* **H. glabra**¹⁰⁰

(5) BORNEO

- 1a. Leaves membranous, usually with irregularly shaped, whitish blotches here and there. Female perianth 2-valved; ovary glabrous. Fruit globose, 1.5-2.0 cm diam., glabrous; pericarp 1-2 mm thick; seed globose. *Plant usually growing not too far from the coast* **H. irya**⁶
 b. Leaves various, usually not white-blotched. Fruit subglobose or ellipsoid; seed ellipsoid. *Plant coastal or not* 2
- 2a. Perianth 2-valved 3
 b. Perianth predominantly 3- (or 4-) valved 5
- 3a. Leaves coriaceous, the lower surface usually densely short-pubescent and with scattered dots and streaks (lens!). Twigs grey-brown, not much contrasting with the colour of the dried petioles **H. crassifolia**⁶⁸
 b. Leaves membranous, the lower surface glabrous and without dots. Twigs greyish or straw, rather contrasting with the blackish colour of the dried petiole 4
- 4a. Female inflorescence \pm spike-like, 5-10 cm long. Perianth persistent under the fruit (always?). *SE. Sabah* **H. sterilis**⁷⁰
 b. Female inflorescence ramified, 1-2 cm long. Perianth not persisting under the fruit. *Sabah, E. & S. Kalimantan* **H. sucosa** subsp. **bifida**^{48b}
- 5a. Leaves in 3 or more rows along the twigs 6
 b. Leaves distichous 8
- 6a. Leaves generally bunched towards the top of the twigs. Petiole proportionally long and slender, 25-50 mm long **H. sabulosa**⁴⁶
 b. Leaves not bunched. Petiole proportionally shorter 7
- 7a. Leaves 10-30 cm long. Twigs pale, greyish or straw, contrasting with the blackish colour of the dried petioles. Female perianth c. 2.5-3 mm long. Fruit 1.5-4 cm long **H. pallidicaula**⁴⁹
 b. Leaves 20-45 cm. Twigs brown, not contrasting. Female perianth c. 4-5 mm long. Fruits 6-8 cm long **H. fragillima**⁸⁶
- 8a. Twigs in apical portion angular, i.e., distinctly lined or ridged from petiole to petiole **H. brachiata**⁷²
 b. Twigs terete or but faintly angular, neither distinctly lined nor ridged 9
- 9a. Leaves on lower surface with persistent tomentum (sometimes largely glabrescent in *H. wallichii*) 10
 b. Leaves beneath glabrous or early glabrescent (midrib sometimes late-glabrescent) 19

- 10a. Plant stout; leaves large, c. 50 cm long, petiole c. 3 mm long only. *Lowland Sarawak* **H. sessilifolia**⁵⁵
- b. Plants various in habit, petiole proportionally much longer 11
- 11a. Older leaves on upper and lower surface with scabrous hair scars. Fruit c. 1.0-1.4 cm long **H. grandis**⁵⁶
- b. Leaves not scabrous. Fruits generally larger 12
- 12a. Leaves on lower surface with scattered dark brown or blackish dots and/or streaks (lens!) **H. wallichii**⁵⁷
- b. Lower leaf surface without dots or streaks 13
- 13a. Perianth with persistent tomentum; perianth not persistent under mature fruit **H. motleyi**⁶⁰
- b. Perianth glabrous or early glabrescent, persistent under the fruit or not .. 14
- 14a. Leaves distinctly bullate due to deep-lying veins and with \pm revolute leaf-margin. *Female flower and fruit not known* **H. reticulata**⁵⁷
- b. Leaves not distinctly bullate 15
- 15a. Ovary pubescent; fruit sometimes pubescent only towards the base 16
- b. Ovary and fruit glabrous 17
- 16a. Twigs moderately stout, 3.5-5 mm diam. towards apex. Leaves 10-23 cm long; nerves 11-16 pairs. Fruit largely glabrescent; perianth not persisting **H. rufo-lanata**⁶⁵
- b. Twigs stout, 4-7 mm diam. Leaves 18-45 cm long, nerves 18-25 pairs. Fruit pubescent, with persisting perianth **H. splendida**⁶⁴
- 17a. Twigs rather stout, towards the apex 3-6 mm diam. Leaves 18-35 cm long; nerves 17-20 pairs. Fruit 2.3-2.7 cm long **H. affinis**⁶⁶
- b. Twigs slender, 1.5-3 mm diam., leaves generally smaller. Fruit c. 1-1.5 cm long 18
- 18a. Leaves membranous; nerves 14-17 pairs **H. gracilis**⁶²
- b. Leaves thinly chartaceous; nerves 5-9 pairs **H. paucinervis**⁶³
- 19a. Lower leaf surface with \pm regularly spaced, brown to blackish dots or with dots and striae (lens!); dots originating from hair scars, not to be confused with usually smaller and irregularly spaced dots or punctation of different origin 20
- b. Lower leaf surface without dots (sometimes with enlarged hair scars) 23
- 20a. Tomentum of leaf bud, the twig apex and young inflorescences composed of hairs c. 0.2 mm long or more 21
- b. Tomentum very short, with hairs c. 0.1 mm long or less 22
- 21a. Twigs conspicuously hollow. Leaves on lower surface often with persistent tomentum. Pedicel at base not articulate. Perianth generally persistent under the fruit **H. wallichii**⁵⁷
- b. Twigs not conspicuously hollow. Lower leaf surface glabrescent. Pedicel at

- base articulate. Perianth not persisting under the fruit **H. borneensis**⁸⁵
- 22a. Twigs rather delicate, diam. towards the apex c. 1.5-2 mm. Leaves c. 5-12 cm long; nerves 8-11 pairs. Fruit 1.1-2.0 cm long, pericarp thin **H. penangiana**⁹⁷
- b. Plant stouter, diam. of twigs towards apex c. 2.5-4 mm. Leaves 9-21 cm long, nerves 11-16 pairs. Fruit 4.5-8 cm long, with thick pericarp **H. punctatifolia**⁹⁸
- 23a. Bark of twigs drying to a pale colour, grey-brown or grey-yellowish, contrasting with the dark brown or blackish colour of the drying petioles 24
- b. Twigs drying brown, not or but contrasting little with the petioles 26
- 24a. Leaves membranous, drying brown or blackish brown, the lower surface somewhat paler. Perianth persisting under the fruit. *Mixed forest* **H. pallidicaula**⁴⁹
- b. Leaves usually chartaceous, drying bright brown or olivaceous, lower surface usually brown or chocolate. Perianth not persisting under the fruit 25
- 25a. Twigs slender, diam. towards the apex c. 2-3 mm. Leaves 7-16 cm long, on lower surface bright brown or chocolate, contrasting well with the grey-olivaceous upper surface. Fruit 1.8-2.7 cm long. *Kerangas forest, peat-forest* **H. oligocarpa**⁹²
- b. Twigs stouter, c. 3-10 mm diam. Leaves 13-35 cm long, the lower surface not conspicuously contrasting in colour. Fruit c. 1.5-2.0 cm long 28
- 26a. Tomentum of leaf bud and immature inflorescence very short, with hairs c. 0.1 mm long or less. Lateral nerves on upper leaf surface flat or sunken, or but little raised 27
- b. Tomentum composed of hairs c. 0.1 mm long or more; lateral nerves raised or not above; if hairs only c. 0.1 mm long, then the lateral nerves, at least in the lower half, distinctly raised above 31
- 27a. Leaves on upper side dull, i.e. on drying the surface finely wrinkling 28
- b. Leaves above not conspicuously dull, surface not finely wrinkling 29
- 28a. Leaves elliptic-oblong to oblong. Fruit c. 1.6-2.0 cm long. *Heath forest, peat swamp forest* **H. carnosa**⁶⁹
- b. Leaves elliptic-oblong to lanceolate. Fruit c. 1.5 cm long. *Mixed forest* **H. tristis**⁵²
- 29a. *Lowland species, up to c. 700 m alt.* Leaves membranous. Fruit 5-5.5 cm long, pericarp thick **H. obscura**⁹³
- b. *Mountainous species; c. 800-1800 m alt.* Leaves membranous or coriaceous. Fruit generally smaller 30
- 30a. Leaves on lower surface without distinct large hair-scars (lens!). Fruit 3-5 cm long **H. subalpina** subsp. **kinabaluensis**^{92b}
- b. Leaves on lower surface usually with distinct enlarged hair-scars. Fruit (immature) c. 1-1.5 cm long **H. xanthina**⁹⁴
- 31a. Pedicels at base not articulate (this character best seen in male flowers).

- Fruit with persisting perianth or not 32
- b. Pedicel at base articulate. Perianth not persisting under the fruit 37
- 32a. Leaves generally large, 15-45 cm long. Fruit c. 6 cm long or more; perianth persisting for a long time under it. *Lowland or mountainous forest* 33
- b. Leaves generally smaller, c. 5-20 cm long. Fruit c. 2-4 cm long; perianth not persisting. *Montane forest at 800-2000 m alt.* 35
- 33a. Nerves 11-22 pairs. *Sabah, Mt. Kinabalu at 1000-1500 m* **H. amplomontana**⁸⁸
- b. Nerves c. 20-30 pairs. *Forests up to c. 1000 m. alt* 34
- 34a. Female flower and fruit not known. *Hallier 624, Mt. Damoes, W. Kalimantan; apparently an undescribed species close to H. valida, see notes* **aff. H. valida**⁸⁴
- b. Female perianth 4-5 mm long. Fruit c. 6-8 cm long, pericarp 10-20 mm thick **H. fragillima**⁸⁶
- 35a. Leaves membranous, apex acute-acuminate. Fruit 2.4-3 cm long **H. androphora**⁸⁷
- b. Leaves chartaceous to coriaceous, apex rounded to (sub) acute, not acute-acuminate 36
- 36a. Leaves chartaceous to coriaceous, lower surface without large hair scars (lens!). Female perianth c. 2 mm long. Fruit c. 2.0-2.7 cm long **H. montana**⁸⁹
- b. Leaves usually strongly coriaceous, usually with large and distinct hair scars on lower surface. Female perianth c. 2.5-3 mm long. Fruit c. 3-4 cm long **H. endertii**⁸³
- 37a. Female inflorescence, female flower and fruit not known. Male inflorescence very stout, the rhachis towards the base 5-8 mm diam. *W. Kalimantan* **H. pachyrachis**⁷³
- b. Male inflorescence less stout 38
- 38a. Midrib on upper leaf surface towards the transition to the petiole c. 3 mm broad or more **H. laticostata**⁷⁹
- b. Midrib at base narrower 39
- 39a. Leaves 16-28 cm long, base short-attenuate to rounded; nerves 16-19 pairs. *Sarawak* **H. nervosa**⁸⁰
- b. Leaves 5-28 cm long, base either rounded or short- or long-attenuate; nerves c. 5-15 pairs 40
- 40a. Lateral nerves on upper leaf surface sunken or flattish, or but slightly raised 41
- b. Lateral nerves distinctly raised above 42
- 41a. Leaf apex rounded. Fruit not seen **H. obtusa**⁷⁵
- b. Leaf apex acute-acuminate. Fruit c. 1.5-2 cm long **H. ridleyana**⁷⁴

- 42a. Tomentum of leaf bud and young inflorescence with hairs c. 0.1-0.2 mm long. Leaves drying dull, greyish-brown, the colours of the upper and lower surface not much contrasting. Fruit c. 1.7-2.0 cm long **H. tenuifolia**⁷⁷
- b. Tomentum of leaf bud c. 0.2 mm long or more; or if c. 0.1 mm long, then the olivaceous to dark brown colour of the dried leaf above much contrasting with the cinnamon colour beneath 43
- 43a. Twigs delicate, towards the apex c. 1-3 mm diam. Leaves generally membranous, 10-18 (-27) cm long. Fruit c. 2.3-2.4 cm long **H. macilenta**⁷⁸
- b. Twigs generally stouter, towards apex c. 2-5 mm diam. Leaves chartaceous, of various size. Fruits of various size 44
- 44a. Twigs early glabrescent; older bark \pm longitudinally cracking. Leaf apex long acute-acuminate. Fruit c. 2.8-3.2 cm long; pericarp hard-woody, 8-10 mm thick. *Brunei* **H. disticha**⁷⁶
- b. Twigs usually rather late glabrescent; older bark striate, not cracking. Leaf apex acute-acuminate, the acumen not conspicuously long. Fruit variable, 1.9-6 cm long. *Whole of Borneo* **H. polyspherula**⁸¹

(6) PHILIPPINES, CELEBES, MOLUCCAS

- 1a. Leaves membranous, usually with irregularly shaped whitish blotches here and there. Female perianth 2-valved; ovary glabrous. Fruit perfectly globose, 1.5-2.0 cm diam., glabrous; pericarp 1-2 mm thick; seed globose. *Plant usually growing not too far from the coast* **H. irya**⁶
- b. Leaves various, usually not white-blotched. Fruit subglobose or ellipsoid; seed usually ellipsoid. *Plant coastal or not* 2
- 2a. Perianth 3-valved. Ovary and fruit glabrous 3
- b. Perianth 2-valved 5
- 3a. Tomentum of leaf bud and inflorescence with hairs c. 0.2-0.6 mm long. Pedicel at base articulated. Fruit c. 2.0 (-2.5) cm long. *Philippines: Mindanao* **H. polyspherula** var. **polyspherula**^{81a}
- b. Tomentum composed of hairs c. 0.1-0.2 mm long. Pedicel not articulated 4
- 4a. Fruit 3.5-7 cm long; dry pericarp 8-15 mm thick. Leaves \pm membranous, drying olivaceous to brown, midrib glabrous above; leaves sometimes with whitish marks as in *H. irya*. *Philippines, Celebes* **H. costulata**⁹¹
- b. Fruit c. 4 cm long, dry pericarp 3.5-8 mm thick. Leaves membranous to thinly coriaceous, drying brown; midrib towards the base in younger leaves pubescent above. *C. Celebes* **H. coriacea**⁹⁶
- 5a. Plant stout; twigs towards apex 4-14 (-20) mm diam., leaves c. 20-45 cm long, petiole short, 2-7 mm long. Tomentum of leaf bud and inflorescence with hairs c. 0.3-1.0 (-1.5) mm long. Female perianth c. 3.5-5 mm long, glabrous; ovary glabrous. Fruit c. 3.5-5.5 cm long, glabrous **H. sylvestris**¹⁹
- b. Plant generally less stout, petiole relatively longer. Tomentum composed of hairs up to 0.2 mm long. Female perianth c. 3.0 (-3.5) mm long or less. Fruit up to 3 cm long, in *H. lancifolia* up to 3.5 cm long 6

- 6a. Leaves \pm chartaceous, oblong-lanceolate to lanceolate. Female perianth at anthesis cleft to c. 1/4; ovary pubescent. Fruit often \pm pear-shaped, 2.5-3.5 cm long, early glabrescent; dry pericarp 4-8 mm thick. *Celebes* **H. lancifolia**³⁷
- b. Leaves of various consistency, generally broader, oblong to oblong-lanceolate. Female perianth at anthesis cleft to c. 1/3 or more. Fruit c. 1.0-3.0 cm long 7
- 7a. Ovary and fruit pubescent; hairs on fruit may be very small and inconspicuous and only remaining at the very base near the insertion of the stalk (lens!). Pericarp thick or thin 8
- b. Ovary and fruit glabrous; dry pericarp thin, c. 1-2 mm. (Female flower and fruit not known in *H. samarensis*¹⁴ and *H. aruana*²⁸) 11
- 8a. Female perianth c. 2.5-3 mm long, at anthesis cleft to c. 1/3-1/2. Fruit (1.6-) 1.8-2.8 (-3.0) cm long; dry pericarp 2-3 mm thick **H. laevigata**³⁵
- b. Female flower not known. Fruit smaller, pericarp thinner 9
- 9a. Fruit 1.5-1.6 cm long, short-ellipsoid. (Male perianth transversely ellipsoid, at anthesis cleft to c. 2/3-4/5). Leaves 8-30 cm long, membranous to chartaceous; nerves flat, inconspicuous. Twigs terete, not ridged. *Talaud Isls. possibly Celebes* **H. talaudensis**¹³
- b. Fruit smaller, c. 1.1-1.3 cm long 10
- 10a. Fruit subglobose. Twigs towards apex \pm flattened, usually lined or lowly ridged from petiole to petiole. Leaves c. 12-25 cm long, membranous; nerves flat, inconspicuous. (Male perianth \pm pear-shaped, cleft to c. 2/3). *Moluccas* **H. decalvata**³⁸
- b. Fruit short-ellipsoid. Twigs terete, not lined. Leaves 5-14 cm long, chartaceous, nerves very inconspicuous on both surfaces. (Male perianth \pm obtriangular, cleft to c. 1/2-way). *Philippines: Luzon* **H. obscurinervia**¹¹
- 11a. Twigs towards apex angular or ridged. (Species distinctive only in male flowering specimens) 12
- b. Twigs terete or subterete, neither angular nor ridged; twigs sometimes faintly angular or shallowly lined from petiole to petiole 13
- 12a. *SW. New Guinea, possibly Aru- and Tanimbar Isls.* (Female flower and fruit not known) **H. aruana**²⁸
- b. *Moluccas: Ceram, Banda, Dammar Isl., possibly Ternate.* (Ovary glabrous) **H. smithii**¹⁵
- c. *Philippines* (Ovary glabrous or almost so) **H. ardisiifolia**¹²
- 13a. Bark of twigs drying pale, grey-brown, contrasting with the blackish colour of the drying petioles. Fruit drying blackish, 1.5-2.0 cm long. *Moluccas* **H. spicata**⁷
- b. Twigs brown, in colour not contrasting with the petiole 14
- 14a. Fruit globose to subellipsoid, 0.9-1.2 cm long; drying blackish. *Aru Isls., New Guinea* **H. subtilis** var. **subtilis**^{20a}
- b. Fruit c. 1.1-1.6 cm long. Fruit not known in *H. samarensis* 15

- 15a. *Philippines: Samar Isls.* **H. samarensis**¹⁴
 b. *Moluccas* 16
- 16a. Fruit ellipsoid, c. 1.5 cm long; drying blackish. *Morotai, Obi Isl.*
 **H. moluccana** var **moluccana**^{9a}
- b. Fruit subglobose or ellipsoid, 1.1-1.6 cm long, drying brown. *Celebes, Kabaena Isl., Ceram* **H. parviflora**¹⁰

(7) NEW GUINEA, SOLOMON ISLS., CAROLINE (PALAU) ISLS., AUSTRALIA

- 1a. Leaves membranous, often with irregularly shaped whitish blotches here and there. Female perianth 2-valved; ovary glabrous. Fruit perfectly globose, c. 1.5-2.0 cm diam., glabrous; pericarp c. 1-2 mm thick; seed globose. *Plant usually growing not too far from the coast* **H. irya**⁶
- b. Leaves of various consistency, generally without whitish blotches. Fruit either ellipsoid or globose; if globose either only c. 1 cm diam. (*H. subtilis*), or the pericarp more than 2 mm thick, at least at one side; seed mostly ellipsoid. Fruit glabrous or pubescent. *Plant coastal or not* 2
- 2a. *Plant from Australia.* Female perianth 2-valved; ovary pubescent. Fruit ellipsoid, 1.8-2.2 cm long, drying orange to brown; pericarp 1-2 mm thick **H. australiana**²⁰
- b. *Plant not from Australia.* Fruit various 3
- 3a. Twigs towards apex distinctly angled or ridged from petiole to petiole. *Aru Isls., New Guinea* 4
- b. Twigs terete, sometimes lined in between the bases of petioles but neither angled nor ridged. *New Guinea to Solomon Isls.* 9
- 4a. Leaves on lower surface with regularly scattered blackish-brown non-traumatic dots or cork warts originating from hair bases (lens!). Perianth 2-valved. *Vogelkop to W. Sepik Dist.* **H. inflexa**⁸
- b. Leaves without blackish-brown dots 5
- 5a. Perianth 3-(or 4-) valved 6
- b. Perianth 2-valved 7
- 6a. Ovary glabrous (?). Fruit 10-16 mm long, glabrous. Leaves chartaceous, 7-14 cm long; petiole relatively long and slender, 11-20 mm long. *SW. and S. New Guinea (Digul; Western Dist.)* **H. olens**¹⁷
- b. Ovary pubescent. Fruit 17-20 mm long, pubescent at base. Leaves membranous to thinly chartaceous, 10-27 cm long; petioles 7-15 mm. *Vogelkop penins.* **H. angularis**²⁶
- 7a. Female perianth depressed-globose, valves nearly 1 mm thick; ovary pubescent. Fruit 17-20 mm long, pubescent. Leaves membranous to thinly chartaceous. *Vogelkop penins.* **H. angularis**²⁶
- b. Female flower and fruit not known 8
- 8a. Leaves membranous. *SW. New Guinea; possibly Aru and Tanimbar Isls.* **H. aruana**²⁸
- b. Leaves thinly coriaceous. *SW. New Guinea* **H. iriana**²⁷

- 9a. Perianth 3-(or 4-) valved; at anthesis cleft almost to the base. *East Sepik Dist.* **H. sepikensis**¹⁸
- b. Perianth 2-valved 10
- 10a. Ovary and fruit glabrous 11
- b. Ovary and fruit pubescent; hairs on fruit either distinct or small and inconspicuous and only to be seen remaining at the base of the fruit near the insertion of the stalk (lens!). Fruit ellipsoid, sometimes in *H. sinclairii* globose 18
- 11a. Tomentum of leaf bud, apex of twig, and inflorescence, with hairs 0.3-1.5 mm long. Leaves large, 17-45 cm long, often \pm parallel-sided, nerves 30-40 pairs. Fruit ellipsoid, 3.4-5.5 cm long, glabrous. *Moluccas and W. & C. New Guinea* **H. sylvestris**¹⁹
- b. Tomentum with hairs c. 0.2 mm long or less; hairs in *H. moluccana*⁹ and *H. tuberculata*³⁹ c. 0.1-0.3 mm long. Leaves generally smaller, nerves fewer 12
- 12a. Fruit globose or subglobose, not beaked and without pseudostalk, c. 1.4 cm diam. or less 13
- b. Fruit ellipsoid, c. 1.3 cm long or more 14
- 13a. Fruit drying brown; dry pericarp c. 1.5-3 mm thick. Female perianth at anthesis cleft nearly to the base. *Northern parts of Irian Jaya and of Papua New Guinea* **H. basifissa**³¹
- b. Fruit drying blackish; dry pericarp c. 1 mm thick. Female perianth at anthesis cleft to c. 1/3. *Aru Isls. Whole of New Guinea* **H. subtilis** var. **subtilis**^{29a}
- 14a. Fruit up to c. 2.0 cm long, drying blackish; top pointed/beaked or not, base without or with long or short pseudostalk 15
- b. Fruit 1.3-3.7 cm long, drying brown or dark brown; top rounded, base without pseudostalk 16
- 15a. Pseudostalk of fruit (1.5-) 2-6 mm long. *Jayapura Dist. (Irian Jaya), W. Sepik Prov.* **H. schlechteri**³⁰
- b. Pseudostalk absent or up to 3 mm long. *Whole of New Guinea* **H. subtilis**²⁹
- 16a. Twigs lined from petiole to petiole. Fruit 2.5-3.0 cm long; pericarp c. 2-3 mm thick, without coarse wart-like lenticels. *Palau Isls.* **H. palauensis**¹⁶
- b. Twigs lined or not. Fruit 1.3-3.7 cm long; pericarp thin or thick, with small or large wart-like lenticels or not 17
- 17a. Female perianth c. 2 mm long, cleft at anthesis to c. 1/2-4/5. Fruit 1.3-2.8 cm long, dry pericarp 1-2 mm thick. *Moluccas, W. New Guinea* **H. moluccana**⁹
- b. Female perianth 2-3 mm long, cleft at anthesis to c. 1/2-2/3. Fruits 1.5-3.7 cm long, pericarp 1-8 mm thick. *Caroline Isls. (incl. Palau), Bismarck Arch., Papuan Isls. and E. New Guinea (Milne Bay Prov.)*. **H. tuberculata**³⁹
- 18a. Arches of the submarginal nerve on the lower leaf surface distinct and very

- regularly looping; nerves often reddish brown. Leaves often \pm parallel-sided. Tomentum of leaf bud composed of hairs c. 0.1-0.3 (-0.4) mm long. Female inflorescence and infructescence up to c. 7 cm long. Fruit 1.7-2.5 (-3.4) cm long, drying orange to brown; pericarp 1-2 mm thick. *Solomon Isls.* **H. whitmorei**³⁴
- b. Marginal nerve not very regularly looping. *Plant not from the Solomon Isls.* 19
- 19a. Tomentum of leaf bud, apex of twigs, and inflorescence short, composed of hairs c. 0.2 mm long or less; in *H. psilantha*³³ hairs c. 0.1-0.3 mm long 20
- b. Tomentum long, with hairs c. 0.5-1.0 mm long; hairs 0.2-0.5 mm long in *H. ampliformis*²⁵; tomentum not known in *H. ampla*²⁴ 28
- 20a. Tomentum of leaf bud composed of hairs c. 0.1-0.3 mm long. Infructescence (and \varnothing inflorescence) large, much branched, 10-16 cm long. Fruit 1.7-2.2 cm long, pericarp thin, 1-2 mm thick, brown. *Bismarck Arch., Bagabag Isl., Long Isl.* **H. psilantha**³³
- b. Tomentum of hairs 0.1-0.2 mm long, or less. Female inflorescence and infructescence c. 10 cm long or less. Fruits various 21
- 21a. Female perianth incl. pedicel long-obconical. Fruit stalk tapering, thickened towards the fruit. Mature fruit not known. *E. New Guinea: Morobe Dist.* **H. crux-melitensis**²¹
- b. Female perianth \pm ellipsoid, well marked off from the slender pedicel. Fruit stalk not tapering 22
- 22a. Fruit 1.6 cm long or less; pericarp 1-3 mm thick. Perianth pubescent 23
- b. Fruit 1.5 cm long or more; pericarp 2 mm thick or more; if fruit c. 1.5 cm long then almost globose and perianth glabrous 25
- 23a. Fruit without pseudostalk, top rounded **H. pilifera**³⁶
- b. Fruit with pseudostalk c. 1.5-5 mm long, top rounded or usually acute, sometimes rostrate 24
- 24a. Leaves drying olivaceous; midrib distinctly raised **H. clavata**²²
- b. Leaves drying dark brown; midrib slightly raised **H. squamulosa**²³
- 25a. Female perianth c. 2-2.4 mm long, glabrous. Fruit (sub)globose, or short-ellipsoid, or obovoid, c. 1.5-2.5 \times 1.5-2.0 cm; pericarp 4-6 mm thick. Leaves 6-14 cm long. *E. New Guinea (Papua New Guinea)* **H. sinclairii**³²
- b. Female perianth c. 2.5 mm long or more, pubescent or glabrescent. Leaves 10 cm long or more 26
- 26a. Fruit 1.6-3.0 cm long, usually with coarse pale-coloured wart-like lenticels; dry pericarp 2-6 mm thick. *Moluccas, New Guinea, and Bismarck Arch.; 0-1000 m alt.* (sometimes much resembling small-fruited *H. pachycarpa*⁴¹) **H. laevigata**³⁵
- b. Fruit (3.0-) 3.5-7.5 cm long; pericarp (4-) 5 mm thick or more. *New Guinea; (450-) 1000-2000 m alt* 27
- 27a. Perianth pubescent. Fruit 3.0-4.5 cm long; pericarp 4-10 mm thick **H. pachycarpa**⁴¹

- b. Perianth glabrescent. Fruit 6-7.5 cm long; pericarp 10-20 mm thick **H. corrugata**⁴⁰
- 28a. Tomentum of leaf bud and inflorescence composed of hairs c. 0.2-0.5 mm long. Female perianth c. 3 mm long, at anthesis cleft to c. 2/3. Fruit not known. Tomentum of leaf bud, female flower and fruit also not known in *H. ampla*²⁴ 29
- b. Tomentum composed of hairs c. 0.5-1.0 (-1.5) mm long. Fruit usually conspicuously pubescent 30
- 29a. Inflorescence glabrescent. *Papua New Guinea: Sepik Prov.* **H. ampla**²⁴
- b. Inflorescence pubescent. *Sepik and Morobe Prov.* **H. ampliformis**²⁵
- 30a. Leaves coriaceous, beneath with harsh hairs, when hairs shed leaving thickened scars. Female perianth c. 4 mm long, at anthesis opening with a narrow pore-like slit at apex. Fruit 3.0-5.0 cm long, pericarp 4-7 mm thick. *New Guinea* **H. pulverulenta**⁴²
- b. Leaves membranous or chartaceous. Perianth at anthesis cleft to c. 1/4-1/2 31
- 31a. Flowers (only the male known) entirely pubescent. Fruit 2.0-2.4 cm long, pericarp 4-7 mm thick. *New Guinea* **H. leptantha**⁴³
- b. Flowers largely glabrescent 32
- 32a. Fruit 2.5-3.0 cm long. Female perianth c. 4 mm long. Leaves generally oblong-lanceolate, at apex caudate. *New Britain* **H. ralunensis**⁴⁵
- b. Fruit 1.2-2.8 cm long. Female perianth c. 3 mm long. Leaves oblong to oblong-lanceolate, at apex not caudate (always ?). *New Guinea and New Britain* **H. hellwigii**⁴⁴

Enumeration and Description of Species

1. *Horsfieldia iryagedhi* (Gaertn.) Warb.

Figs. 1A(1); 2 I; 3.

Myristica iryagedhi Gaertn., De Fruct. et Sem. Pl. 1 (1788) 196, t. 41, f. 4 — *Horsfieldia iryagedhi* (Gaertn.) Warb., Mon. Myrist. (1897) 332, t. 21 fig. 1-4; Sinclair, Gard. Bull. Sing. 28 (1975) 68 — Type: Gaertner's drawing.

? *Phelima Noronha*, Verh. Batav. Genootschap Kunsten en Wetenschappen 5, art. 4 (1790) (3) et (edit. 1827) 66, *nom. nud.*

M. glomerata Thunb., Acta Holm. sive Vet. Akad. Nya Handl. (1799) 88, t. 2, f. 1 (*non* Miq., 1852) — Type: Herb. Thunberg, n.v.; microfiche: fragment of male inflor.

H. odorata Willd., Sp. Pl. (ed. 4) 4, 2 (1805) 872 — Type: not known (see Sinclair, l.c.).

M. horsfieldii (first spelling *horsfieldia*) Bl., Bijdr. 2, 11 (1826) 577; Rumphia 1 (1837) 192, t. 63; King, Ann. Roy. Bot. Gard. Calc. (1891) 296, pl. 122, 123 — *Pyrrhosa horsfieldii* (Bl.) Hasskarl, Cat. Pl. Hort. Bog. (1844) 174. — Type: *Blume s.n.*, Java (L).

M. notha auct. *non* Wall. Koenig ex Bl., Rumphia 1 (1837) 192, *nom. nud. pro syn.*

Myristica (Cnema) glomerata Miq., Pl. Jungh. (1852) 170 (*non* Thunb., 1799) — Type: *Junghuhn s.n.*, Java (U; iso L).

Myristica odorata Reinw. ex de Vriese, Pl. Ind. Bat. Or. 2 (1857) 95 (*non odorata* Willd.), *nom. nud. pro syn.*

For further references see Sinclair, l.c.

Tree 5-25 m. Twigs terete, not ridged, towards the apex 2-5(-14) mm diam., at first with woolly tomentum, of rust-yellow hairs c. 0.5 mm, twigs early to late glabrescent, bark grey-brown, rather coarsely striate, lower down coarsely striate or longitudinally cracking, rarely somewhat flaking; lenticels usually present but sometimes inconspicuous. Leaves in 2 rows, chartaceous, ovate-elliptic to oblong-lanceolate, broadest usually at about the middle, 10-28 × 4-12 cm, base rounded to attenuate, top acute-acuminate, upper surface glabrous, usually drying dark brown, or dark olivaceous, lower surface early or late glabrescent, without brown-black dots, the epidermis always finely papillose; midrib above often late-glabrescent, flat or slightly raised; nerves 9-16 pairs, above flat or sunken, the lateral arches not very distinct; tertiary venation forming a coarse network, usually ± trabeculate, above distinct to hardly visible; petioles late-glabrescent, 15-20 (-25) × 2-3 mm; leaf bud c. 10-15 × 3-4 mm, densely pubescent with hairs c. 0.5 mm long. Inflorescences densely woolly pubescent with hairs c. 0.3-0.5 mm, in ♂ : c. 6-15 × 4-10 cm, usually twice ramified, the branches rather few, thickish, common peduncle c. 0.3-2.0 cm, the flowers united into c. 10-25 subglobose dense clusters or capituli c. 5-10 mm diam., each with c. 80-100 flowers, the capituli being rather spaced along the branches; ♀ inflorescences smaller, little-branched, c. 1.54- × 1.5-2 cm, the flowers solitary or a few together; bracts broadly ovate or ± triangular to elliptic, the larger ones with distinct midnerve, c. 1-3 mm long, pubescent, caducous. Flowers in ♂ : 3 (or 4)-valved, in ♀ : 3 (or 2)-valved; perianth glabrous except towards the very base; pedicel short or absent, pubescent, at base not articulated. Male perianth narrowly ± obovoid-oblong or obconical, 3-5 (or 6)-angular, c. 2-2.5 × 1-1.6 mm, top broadly rounded, gradually tapering to the base, glabrous but with a few hairs c. 0.2 (-0.5) mm long at the transition to the pubescent pedicel: 0-0.2 (-0.3) mm long; perianth at anthesis cleft at first to c. 1/5-1/4, in adult usually up to c. 3/4; valves c. 0.2 (-0.3) mm thick. Androecium elongate, narrowly obconical or blunt ellipsoid-oblong, top ± truncate, base tapering, c. 1.0-1.2 × 0.4-0.5 mm; anthers 3-5 (i.e., 6-10 thecae), largely sessile, erect, free apices c. 0.2 mm, central column narrow, hollow to about half-way, androphore narrow, c. 0.2-0.5 mm long. Female perianth broadly ellipsoid, c. 3 × 2 mm, at anthesis cleft to c. 1/2-way, valves c. 0.3 (-0.5) mm thick; ovary broadly ellipsoid, c. 2.0 × 1.5 mm, densely short-pubescent, stigma minutely 2-4 (or more)-lobulate; pedicel absent or up to 0.2 mm. Fruits 3-8 in a cluster, ellipsoid to ellipsoid-oblong, top and base broadly rounded, c. 2.5-4.2 × 1.7-2.4 cm, densely rust-yellowish pubescent with stellate-dendroid hairs c. 0.5 mm, sometimes partly glabrescent, pericarp dark brown, not tuberculate, c. 1.5-2.0 (-3.0) mm thick; stalk 0.5-2 mm long; perianth not persisting under the fruit.

Distribution: Ceylon, introduced in Malaya (Penang Isl.), Singapore, Java.

CEYLON: *Balakrishnan NBK 935; Burman s.n., 33; Davidse & Sumithraarachchi 8539; herb. Hooker s.n.; Huber s.n.; Jayasuriya & Bandaranaike 1869; Kostermans 23321; 24114, 26670, 27113; Meijer 268, 276; Nooteboom (& Huber) 3164, 3188; herb. Pallas 51; herb. van Royen s.n.; Thwaites C.P. 221; Waas 743, 892; Walker s.n.; White & Arnott s.n.; Worthington 2130, 2291, 2325, 2345, 2346, 2582, 3533, 3535, 4124, 4832, 5201, 5228, 6023, 6474, 6580.*

SINGAPORE (cult): *Walker 267.*

JAVA (cult, mainly W. Java): *Backer 36342; Bakhuizen van den Brink 7319, 7409; Blume s.n.; van Heurn s.n.; Junghuhn s.n. (42); Koorders 31019 β; Korthals s.n.; Martati (133); Radermacher 93; herb. Reinwardtianum 154; Teysmann s.n.; de Vriese s.n.; Zollinger 3263 (? 3268).*

Ecology. Lowland rain forest, wet evergreen forest, "intermediate" forest; also in disturbed forest; 0-500 m. Flowers and fruits throughout the year.

Vernacular names. *Ruk, Rukghedhi* and *Malaboda* (Ceylon); *Irie gaga* (Ceylon, König ms.); *Tjampaka sèlong* (Java, Soenda).

Uses. Formerly in Java a wax was obtained from cooking the fruits. The wood is moderately heavy and even-grained (see Sinclair, p. 72).

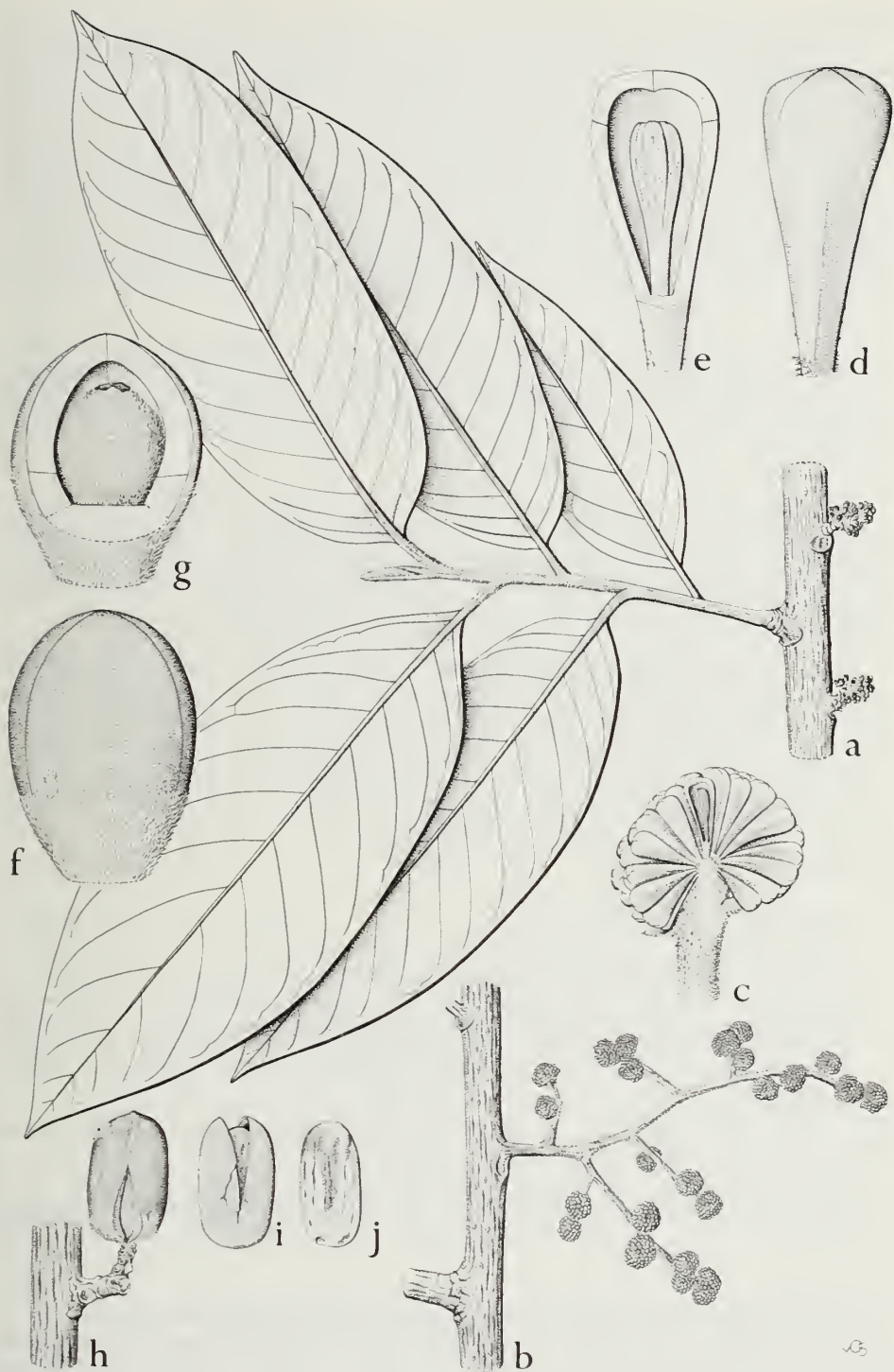


Fig. 3 *Horsfieldia iryaghedhi* (Gaertn.) Warb.
a. habit of twig with leafy shoot and female inflorescences, $\times 1/2$; *b.* twig portion with male inflorescence, $\times 1/2$; *c.* subspherical male flower head, flowers partly removed, one flower opened, $\times 3$; *d.* mature male flower bud, lateral view, $\times 12$; *e.* ditto, longitudinal section showing androecium, $\times 12$; *f.* mature female flower bud, $\times 12$; *g.* ditto, opened, showing pubescent ovary and sessile, minutely lobulate stigmas, $\times 12$; *h.* infructescence, $\times 1/2$; *i-j.* seeds with and without seed coat, $\times 1/2$. — *a, f, g* from Anon., Hort. Bot. Sub. XIII-E-9; *b-e* from *Jayasurya & Bandaranaike* 1869; *h-j* from *Kostermans* 26670.

NOTES

1. *Fieldnotes*. Trees to c. 25 m tall, at base to c. 50 cm diam., branches drooping, sometimes branched from the base. Stilt roots sometimes present when growing in wet soil. Bark hard, outerbark light brown or black-brown or greyish-red, fissured or gritty, or peeling off in large pieces, or smooth; living bark 5-10 mm, beefy red or red brown, with white lines, exuding a clear light reddish brown sap; wood white to light yellow with red streaks. Leaves grey-green beneath. Perianth yellow or dark yellow, or orange brown; pistil with brown hairs. Fruits yellow or yellowish brown with rusty tomentum; aril complete, orange to deep red. Fresh male flowers c. 3 mm long; flowers strongly scented, reminiscent of that of *Michelia champaca*, according to Sinclair emanating again on boiling the dried flowers.

2. This species rather deviates from all other *Horsfieldias*, and is now placed by me in a separate section. It is mainly distinct by the leaves being papillate beneath, male flowers arranged in compact heads, rather-many-lobulate stigma; and according to Warburg (p. 334), the seed contains some starch, which seems to be unique for this species of *Horsfieldia*.

According to Sinclair (l.c.) its closest relative might be *H. wallichii* because in that species, before anthesis the flowers are almost sessile and clustered as well, and because of similar leaves. However, when mature, the flowers of *H. wallichii* are quite different, especially because of the much broader androecium; also, its leaves have typical minute dots and stripes beneath, but are not papillose.

Warburg placed *H. iryaghedhi* and *H. sylvestris* in a section *Orthanthera* because the flowers are similarly arranged into small dense capitula in the later species. At full anthesis, however, the flower heads of *H. sylvestris* loosen considerably and their inflorescences then link up with other *Horsfieldias*.

The arrangement of flowers in heads somewhat resembling dense capitula is found in the African genus *Pycnanthus* and the genus *Brochoneura* from Madagascar.

2. *Horsfieldia kingii* (Hook. f.) Warb.

Figs. 1A(2); 4.

Myristica kingii Hook. f., Fl. Br. Ind. 5 (1886) 106; King, Ann. Roy. Bot. Gard. Calc. (1891) 300, pl. 127; Kanjilal & Das, I l. Assam 4 (1940) 43; C.Y. Wu, Fl. Yunnanica 1 (1977) 10, fig. 4 (9-10); Tsiang Li & Li, Fl. Rep. Popul. Sin. 30, 2 (1979) 202, fig. 92 — *Horsfieldia kingii* (Hook. f.) Warb., Mon. Myrist. (1897) 308; Sinclair, Gard. Bull. Sing. 28 (1975) 74. — Type: *King s.n.* (Sikkim, 19th June 1881) (CAL, *n.v.*; K, iso; BM: G, *n.v.*, lecto); *Masters s.n.* CAL, *n.v.*; K, iso; L, P; BO, DD, M, PDA, *n.v.*).

H. hainanensis Merr., Lingnan Sc. J. 11 (1932) 43; Tsiang, Li & Li, Fl. Rep. Popul. Sin. 30, 2 (1979) 199, fig. 91 — Type: Tsang & Fung 17851 (NY, *n.v.*; iso K).

H. tetratypala C.Y. Wu, Acta Phytotax. Sin. 6 (1957) 218; Fl. Yunnanica 1 (1977) 12, fig. 4(1-8); Tsiang, Li & Li, Fl. Rep. Popul. Sin. 30, 2 (1979) 197, fig. 90 — Type: Exp. Sino-ross. Yunnan 2770 (KNN, PE, *n.v.*).

Tree 6-25 m. Twigs terete (not ridged) towards the upper 4-10 (-12) mm diam., bark dark brown, rather early glabrescent, tomentum grey-brown to light brown, hairs c. 0.2-0.4 mm long, bark lower down \pm coarsely striate, not flaking; lenticles usually distinct. Leaves in (3-) 5 rows, membranous to chartaceous, (obovate to) elliptic-oblong to oblong-lanceolate, broadest at or usually somewhat above the middle, 12-35 (-55) \times 5-17 (-22) cm, base attenuate, top acute-acuminate; upper surface drying dark olivaceous-brown to dark brown; lower surface largely early glabrescent but usually some tomentum vestigial for a while on and near the midrib, without brown-black dots; midrib flat above; nerves 13-18 pairs, flat or slightly sunken above, marginal arches indistinct; tertiary venation forming a coarse network generally faintly visible above; petioles (9-) 15-25 \times (2-) 2.5-4 mm, glabres-

cent rather late; leaf bud c. $15-20 \times 3-4$ mm, densely grey brown to pale brown pubescent with hairs c. 0.2-0.4 mm. Inflorescences rather thinly woolly-pubescent with greyish to pale brown hairs c. 0.2-0.4 mm, in δ : rather slender to broad, 2-3 times ramified, flowers moderate to rather few, c. (5-) $7-16 \times 3-8$ (-12) cm, common peduncle c. 10-20 mm long; in η : 1-2 times ramified, rather few-flowered, 2-8 cm long; bracts oblong to lanceolate, pubescent, 3-10 mm long, caducous. Flowers in male (see notes to the synonyms) 2- or usually 3- or 4- (or 5-) valved, in η either 2- or 3-valved, in δ arranged in loose or dense clusters of 3-10, in η c. 1-3 together; perianths pubescent with soft hairs 0.1-0.3 mm long, or partly glabrescent; pedicels pubescent to subglabrescent, at base not articulated. Male perianth in mature bud globose or subglobose, usually slightly angled on the valve-sutures, c. $2.5-3.5 \times 3.0-4.0$ mm, top rounded or slightly acute, base broadly rounded; pedicel stoutish, 1.0-2.0 (-2.5) mm long; perianth at anthesis cleft to $2/3-3/4$, valves 0.5-0.8 mm thick, sometimes rather coriaceous. Androecium depressed-globose or depressed and broadly obovoid, top broadly rounded to subtruncate, c. $1.0-1.6 \times 1.5-2.0$ mm, in transverse section subcircular to bluntly 3- (or 4-) angular; anthers (12-) 14-16 (-20), largely sessile, free apices c. 0.1-0.3 mm, towards apex curved over and into the rather broad apical cavity, cavity c. 0.3-0.8 mm deep; androphore rather narrow, c. 0.1-0.3 mm long. Female perianth 2- or 3-valved, ovoid-ellipsoid, $3.0-4$ (-5) $\times 3.0-3.5$ mm, thinly pubescent or subglabrescent, at anthesis cleft to c. $1/2$ -way, valves c. 0.6 mm thick, \pm coriaceous, ovary ellipsoid or obovoid, c. $2.0-2.5 \times 2.0$ mm, pubescent, stigma minutely 2-lobed, 0.1-0.2 mm long, pedicel 2-3 mm long. Fruits 1-6 per infructescence, ellipsoid to ellipsoid-oblong, top rounded to (sub) acute, base narrowly rounded to rather long-tapering, c. (3-) $4-6 \times 2-2.7$ cm, dry pericarp 3-4 mm thick with granulate-striate surface, drying dark brown, glabrescent early; stalk 3-8 mm; perianth persisting.

Distribution. India (Assam, Sikkim), E. Nepal, Bangladesh (? , no specimens seen), Burma (? , no specimens seen), China: Yunnan, Kwangsi (no specimens seen), Hainan.

INDIA. Bengal: *Haines 842* — Assam: *Masters s.n.*; herb. *Pierre 5462* — Sikkim: *Gammie, King's Coll. s.n.*; *King 2380*; *Rogers s.n.*

E. NEPAL: *Stainton 6436, 6880.*

CHINA. Yunnan: *Henry 12.234* — Hainan: *Tsang & Fung (317) L.U. 17851.*

Ecology. Lower montane forest, in gullies of evergreen forest; 300-1200 m alt. Flowers and fruits probably throughout the year.

Vernacular names. (See Sinclair, p. 75) *Amol* (Assam); *Mijing-ikum-asing* (Miri); *Pandikachophang* (Kach.); *Siltui* (Lushai); *Bolong, Bolouchi* (Garo).

Uses. Kernel used as a substitute for areca nut in betel chewing. The gum is good against mouthsores.

NOTES

1. *Fieldnotes.* Bark grey or brownish, somewhat rough, flaking in small square flakes, and longitudinally fissured; sap blood red. Male flowers recorded as orange-red, fruits as yellow.

2. *Synonyms.* In the *Flora of China* (Fl. Rep. Popul. Sin.) (1979), besides *H. kingii* two related species *H. tetratopala* and *H. hainanensis* are accepted. I have seen no material of *H. tetratopala* and *H. hainanensis* only the sterile isotype in K, and some separate flowers of the same collection kindly procured by the herbarium at Berkeley, but after studying the descriptions and the figures in the *Flora of Yunnan* (1977) and the *Flora of China* (1979) I see no reason to keep them separate. In the *Flora of China* the three species are keyed out on vegetation

characters viz., the presence or absence of lenticels on the twigs, the degree of persistence of the tomentum on the lower midrib, the number of lateral veins (which strongly overlap), and the length of the infructescences: 6-12 cm in *H. tetratepala* and 2-4 cm in *H. hainanensis*.

However, the following remarks should be made.

1. *H. tetratepala*: in the *Flora of Yunnan*, figure 4, 3-4, a distinct cup-like disk under the androecium is visible, whereas in the figure of the same species in *Flora of China*, figure 91, this cup-like disk is absent. If, in fact, a disk is present, comparable to the one present in the Malayan *Knema plumulosa*, then this would be a strong argument to regard *H. tetratepala* as a distinct species.

2. *H. kingii*. In *Flora of China*, figures 92, 2, the male perianths were drawn as glabrous and 2-valved, whereas for *H. tetratepala* and *H. hainanensis* they are presented as pubescent and 3- or 4- (or 5-) valved. The perianths in the type of *H. kingii*, however, being also pubescent and 3-valved indicate this species be regarded as conspecific. If in the specimens used for the drawing of what is called *H. kingii* in *Flora of China* the male flowers are truly glabrous, and 2-valved, this would be a reason for further investigation on the status of these specimens, which might represent a new taxon.

3. *Henry 12.234* from Yunnan, a good male flowering collection, was identified by Sinclair as *H. macrocoma*, for reasons unclear to me, possibly because of the rather slender male inflorescences.

3. *Horsfieldia longiflora* de Wilde, *sp. nov.*

Fig. 1A(3)

Horsfieldia amygdalinae affinis, differt foliis distichis, perianthiis masculis 2-valvibus, \pm ellipsoideis parum compressis, c. 2-3 mm longis, androecio c. 2.0×1.3 mm, antheris 10-12, fructibus breviter ellipsoideis, c. 1.5×1.2 cm. — Type: *Eberhardt 3050* (P).

Tree 6-20 m. Twigs terete, not ridged, towards the top 2.5-6 (-10) mm diam., bark dark grey-brown to blackish brown, tomentum with hairs c. 0.1 mm long or less, grey-brown, early glabrescent, lower down the bark coarsely striate, not flaking, lenticels distinct. Leaves in 2 rows, membranous to chartaceous, elliptic-oblong to oblong-lanceolate, broadest at about the middle, $7-21 \times 3-7.5$ cm, base attenuate, top acute-acuminate; upper surface drying olivaceous brown to dark brown; lower surface glabrescent early, without larger dark brown dots; midrib flattish above to slightly raised; nerves 9-13 pairs, flat to slightly raised, or sunken above, marginal arches indistinct; tertiary venation forming a lax network, faint or invisible above, usually faint beneath; petioles $9-12 \times 1.5-2.5$ mm, glabrous; leaf bud slender, $10-14 \times 2-3.5$ mm, densely grey-brown pubescent with hairs c. 0.1 mm long or less. Inflorescences with sparse tomentum of hairs c. 0.1 mm or less, subglabrescent, in δ : c. 3 times ramified, moderately- to many-flowered, c. $6-10 \times 4-6$ cm, common peduncle 6-20 mm; in η : 1-2 times ramified, c. 2-3 cm long; bracts \pm elliptic, short-pubescent, 2-5 mm long, caducous. Flowers 2-, rarely with a few 3-valved, the δ in loose clusters of 3-6, the η c. 1-3 together, glabrous; pedicels glabrous, at base not articulated. Male perianth in bud with frontal view broadly ellipsoid-obovoid, laterally somewhat flattened, $2.2-3.0 \times 1.8-2.0$ mm, 1.2-1.5 mm thick, top broadly rounded, base shortly rounded to subattenuate, outside faintly longitudinally ribbed or not; pedicel slender, 1-2 mm long; perianth at anthesis cleft to nearly 1/2-way, valves c. 0.2 mm thick. Androecium flattened, obovoid-ellipsoid, top broadly rounded to subtruncate, $1.7-2.0 \times 1.0-1.3 \times 0.6-0.8$ mm, in transverse section ellipsoid; anthers 10-12, sessile, free apices c. 0.1 mm, suberect or little incurved; apical cavity narrow, 0.2-1.0 mm deep; androphore rather broad, tapering, c. 0.2-0.3 mm long. Female perianth ovoid-ellipsoid, c. 2.5×2.0 mm, glabrous, at anthesis cleft to nearly 1/2-way, valves c. 0.3 mm thick, ovary ovoid, c. 1.8×1.5 mm, glabrous, stigma minutely 2-lobed, c. 0.1 mm long, pedicel c. 1.0-1.5 mm long.



Fig. 4. *Horsfieldia kingii* (Hook. f.) Warb.
a, leafy twig with male inflorescences, note dispersed leaves, x 1/2; *b*, mature male flower bud, lateral view, x 6; *c*, ditto, opened, showing androecium, x 6; *d*, androecium, longitudinal section, schematic, x 6; *e*, mature female flower bud, x 6; *f*, ditto, opened, showing pubescent ovary with minute bi-lobed stigma, x 6; *g*, twig portion with infructescence, note persistent perianth under fruit, x 1/2. — *a-d*, from Haines 842; *e* & *f*, from Tsang & Fung 317; *g*, from King's Coll. s.n. (Sikkim).



Fig. 5. *Horsfieldia thorelii* Lecomte
a, twig with leaves and male inflorescences, note dispersed phyllotaxis, x 1/2; *b*, mature male flower, lateral view, x 12; *c*, ditto, opened, showing androecium, x 12; *d*, androecium, longitudinal section, schematic, x 12; *e*, twig portion with female inflorescences, x 1/2; *f*, mature female flower, lateral view, x 6; *g*, ditto, opened, showing glabrous ovary, x 12; *h*, twig portion with infructescence with immature fruits, x 1/2; *i*, mature fruit, x 1/2. — *a-c*, from Poilane 19887; *e-g*, from Maxwell 75-212; *h* & *i* from Poilane 22394.

Fruits 1-8 per infructescence, broadly ellipsoid, top and base rounded, c. 1.5×1.2 cm, surface granulate, not tuberculate, drying dark brown, glabrous, dry pericarp c. 1 mm thick; stalk 1.0-1.5 mm long; perianth not persisting.

Distribution: C. Vietnam (Annam)

VIETNAM. Annam: *Clemens* 3474; *Eberhardt* 3050; *Polane* 10224, 13529, 29315.

Ecology. Submontane evergreen forest, on rather poor soil; exact altitudes not recorded; flowers March to May, fruits May-July.

Vernacular names. Lan Ham, Cõn na ham (Moi), Mẽ tũóng.

Uses. Leaves are used for bathing after childbirth. The wood is recorded as soft and light.

NOTES

1. Flowers yellow, fruits red.

2. Closely related to *H. amygdalina* and *H. thorelii*, both differing by the shorter and smaller male flowers with differently shaped androecium (but see note 3 under *H. amygdalina*), and by the larger fruits. In *H. longiflora*, however, fruits are known only from one collection (*Clemens* 3474). All specimens of our present species have the leaves distichous; in *H. thorelii* all specimens have the leaves dispersed, in *H. amygdalina* both distichous and dispersed phyllotaxes can be found.

3. Sinclair included the specimens of the present new species in his broadly conceived *H. glabra*. The specimens were all collected after the treatment in the Flore Générale de l'Indo-chine (1914).

4. *Horsfieldia thorelii* Lecomte

Figs. 1A(4); 5.

H. thorelii Lecomte, Not. Syst. 1, 4 (1909) 99; Fl. Gén. 1-C. 5, 2 (1914) 100; Sinclair, Gard. Bull. Sing. 16 (1958) 422 (See note, in syn. of *H. amygdalina*) — Type: *Thorel s.n.* and 1186 (P) (some of the duplicates are *H. irya*).

Tree 4-20 m. Twigs terete, not ridged, towards the top 2.5-6 (-12) mm diam., bark dark grey-brown to dark brown, early glabrescent from a grey-brown to rusty tomentum with hairs c. 0.1-0.3 mm, bark lower down finely to \pm coarsely striate, not flaking, lenticels small, generally inconspicuous. Leaves in 3-5 rows, membranous to chartaceous, elliptic-oblong to oblong, broadest at or somewhat above the middle, $9-23 \times 3-9.3$ cm, base attenuate, top acute-acuminate; upper surface drying olivaceous-brown to blackish brown; lower surface early glabrescent, without brown dots; midrib slightly to much raised above; nerves 9-13 pairs, flat to moderately raised above, marginal arches not distinct; tertiary venation forming a coarse network, usually faint to invisible on both surfaces; petioles $6-17 \times 1.5-3.5$ mm, glabrous; leaf bud slender to rather stout, c. $8-16 \times 2-4$ mm, densely greyish brown to rusty-pubescent with hairs c. 0.1-0.3 mm. Inflorescences \pm thinly pubescent with hairs c. 0.2-0.5 mm, sometimes subglabrescent, in σ : 3-4 times ramified, many-flowered, $4-22 \times 2-12$ cm, common peduncle c. 10-30 (-75) mm; in φ : 1-2 times ramified, c. 2-6 cm long; bracts oblong to lanceolate, pubescent, c. 2-4 (?) mm, caducous. Flowers either predominantly 2-valved or in mixture of 2- and 3-valved, the σ in rather dense clusters of c. 5-12, the φ c. 1-4 together; perianths glabrous; pedicel glabrous, in σ at base not articulated, in φ articulated or not (see notes). Male perianth broadly obovoid to globose or depressed globose, top broadly rounded, base rounded to broadly rounded, outside faintly longitudinally ribbed or

not, c. 1.0-1.5 (-1.7) \times 1.2-2.0 mm; pedicel 0.4-1.0 (-1.5) mm, slender; perianth at anthesis cleft to c. 1/2-way, valves 0.1-0.2 mm thick. Androecium depressed-obovoid to (depressed)globose, c. 0.6-1.0 \times 0.6-1.1 mm, usually somewhat laterally flattened and hence subcircular to elliptic (not circular) in transverse section; anthers 7-9 (-10), sessile, free apices 0-0.1 mm, towards the apex incurved over a rather narrow central cavity c. 0.1-0.4 mm deep; androphore narrow, 0.1-0.2 mm long. Female perianth obovoid-ellipsoid, 1.8-2.5 \times 1.6-2.2 mm, glabrous, at anthesis cleft to c. 1/3, valves 0.3-0.4 mm thick, ovary ellipsoid, 1.4-1.7 \times 1.0-1.4 mm, glabrous, stigma minutely 2-lobed, c. 0.1 mm, pedicel 1-1.5 mm long, glabrous or thinly pubescent. Fruits 1-5 per infructescence, broadly ellipsoid, top and base broadly rounded, 1.8-3.2 \times 1.5-2.4 cm, finely granulate, not tuberculate, drying dark brown, glabrous, dry pericarp c. 1.5-2.5 mm thick; stalk c. 1-2 mm; perianth not persisting.

Distribution. Vietnam (Annam, Cochin-China), Laos, Cambodia, S. and SE. Thailand (not in peninsula).

VIETNAM. Annam: *Poilane* 8699, 18160, 18308, 18615, 19887, 22394 — Cochin-China: *Chevallier* 39134, *Pierre* 14, 1812, 5434, *Poilane* (56), *Thorel* s.n., 1186.

LAOS. *Poilane* 13480.

CAMBODIA. *Hahn* 140, *Pierre* 680, *Poilane* 23253, 23341, *Vidal* 5044.

THAILAND. *Maxwell* 74-794, 75-212, 76-158, 76-429, *Smitinand & Phengklai* 10870.

Ecology. Evergreen forest, regenerating forest; on rich red soil; 200-1100 m alt. Flowers and fruits throughout the year.

NOTES

1. Latex from bark colourless. Leaves subcoriaceous. Flowers yellow; fruits greenish-yellow; aril thin, orange.

2. Female flowers have only been seen from two rather differing collections, viz., (1) an unnumbered specimen collected by *Poilane* (10) (Indo-China), which deviates somewhat in habit from the other specimens by its rather narrow lanceolate leaves c. 18 \times 4.5 cm, and slender inflorescences of c. 6 cm long with immature flowers with the pedicels glabrous and articulated at the base; (2) *Maxwell* 75-212, from Thailand, with stouter and more condensed inflorescences, with stouter flowers of which the pedicels thinly pubescent towards the base and not articulated; possibly the articulation of the pedicels in the *Poilane* specimen is artificial and caused by the drying of the immature flowers.

3. *H. thorelii* is mainly characterized by the leaves being always dispersed in 3-5 rows, and by the very small globose male flowers c. 1.0-1.5 mm diam. It is closely related to the polymorphous *H. amygdalina*, a species with a larger distributional area and differing by having larger, male perianths (c. 1.5-2.3 mm long), generally more anthers (8-15), and slightly larger fruits (2.2-3.4 cm long); it is also closely related to *H. longiflora*, but the latter species differs by its larger and more elongate flowers, smaller fruits, and generally distichous leaves.

4. *Poilane* 23252, 23341, and *Vidal* 5044, from Cambodia, Prov. Kampot, alt. c. 200-300 m, are specimens deviating by the poor and short pubescence (hairs c. 0.1 mm) of the inflorescences; similar short-haired, glabrescent inflorescences have been collected in in Thailand e.g., *Maxwell* 74-794.

5. *H. thorelii* seems to replace *H. amygdalina* in Annam and Cochin-China (Central and S. Vietnam).

6. In 1956 Sinclair (p. 422) regarded *H. thorelii* as a synonym of *H. amygdalina*; in 1975 (p. 42) both these names were reduced to his wide conception of *H. glabra*.

5. *Horsfieldia amygdalina* (Wall.) Warb.

Myristica amygdalina Wall., Pl. As. Rar. 1, 4 (1830) 79, t. 90; Cat. (1832) No. 6797; Hook. f. & Th., Fl. Ind. (1855) 160, p.p.; King, Ann. Roy. Bot. Gard. Calc. 3 (1891) 300, pl. 128. — *Horsfieldia amygdalina* (Wall.) Warb., Mon. Myrist. (1897) 310; Sincl., Gard. Bull. Sing. 16 (1958) 422 (in syn. and in notes to *H. bracteosa*); C.Y. Wu (Ed.), Fl. Yunnan. 1 (1977) 12, fig. 3, 5-6 — Type: Wallich. Cat. 6797 (KW; K, iso; BM: CAL, G, n.v.).

Myristica floribunda Wall., Cat. (1832) no. 6805, *nom. nud.*

M. kurzii King, *nom. nud.* (sub *M. glabra auct. non Bl.*: King). — Type: Kurz s.n., 984 (CAL, n.v.; iso, P).

Horsfieldia tonkinensis Lecomte, Not. Syst. 1, 4 (1909) 100; Fl. Gen. 1.-Chine 5, 2 (1914) 101 — Type: Bon 4272 (4302) (P).

H. tonkinensis var. *multiracemosa* Lecomte, Not. Syst. 1, 4 (1909) 100; Fl. Gén. 1.-Chine 5, 2 (1914) 102 — Type: Bon s.n. (4302) (P).

Myristica glabra auct. non Bl.: King, Ann. Roy. Bot. Gard. Calc. 3 (1891) 310, pl. 142 — *Horsfieldia glabra auct. non (Bl.)* Warb.: Sinclair, Gard. Bull. Sing. 28 (1975) 35, p.p. (as for most of the specimens originating from continental Asia); Fl. Rep. Pop. Sin. 30, 2 (1979) 204, fig. 93.

H. prunoides C. Y. Wu, Yunnan Econ. Pl. (1973) 74, fig. 56, *nom. nud.* — Type: publication not seen; name cited in the synonymy of *H. glabra auct.* in Flora of China, 1979.

Tree 5-30 m. Twigs terete, not ridged, towards the top 1.5-3.5 (-8) mm diam., bark grey-brown to brown, tomentum greyish to brown, composed of hairs c. 0.1-0.2 mm (var. *amygdalina*) or c. 0.5-1.0 mm long (var. *lanata*), usually tomentum early glabrescent, lower down the bark rather finely striate, not flaking; lenticels small, \pm conspicuous or not. Leaves either in 2, or 3, or 5 rows, or phyllotaxes mixed, membranous to subchartaceous, elliptic-oblong to oblong, broadest at about or slightly above the middle, 9-23 \times 2.5-7.5 (-9) cm, base attenuate, tip acute-acuminate; upper surface drying olivaceous brown to dark brown; lower surface early glabrescent, without brown or blackish dots; above, midrib flat to moderately raised; nerves 7-14 pairs, thin, either sunken or flat, or moderately raised, marginal arches not distinct; tertiary venation forming a rather lax network, usually faint to invisible on both surfaces; petioles 10-20 \times 1.5-3.5 mm, glabrous; leaf bud slender to stoutish, densely grey-brown to brown, pubescent with hairs 0.1-0.2 or 0.5-1.0 mm (see under the varieties), c. 10-15 \times 1.5-4 mm. Inflorescences either very thinly pubescent with pale hairs c. 0.1 mm (var. *amygdalina*) to early glabrescent or early glabrescent and hairs densely set, rusty, c. 0.5 (-1.0) mm (var. *lanata*), in δ : 3-4 times ramified, flower-number moderate to many, 6-18 \times 3-12 cm, common peduncle 7-40 mm; in φ : 1-2 times ramified, 1-3 (-6) \times 1-1.5 (-4) cm; bracts \pm elliptic, tip rounded, pubescent, 1-2 (-3) mm long, caducous. Flowers either 2- or 3- (or 4-) valved, or \pm an even mixture of 2- and 3-valved, in δ rather dispersed or in loose clusters of 4-10, in φ solitary or 2-3 together, glabrous; pedicels glabrous, at base not articulated, or in φ sometimes indistinctly articulated. Male perianth shortly obovoid or short-ellipsoid to globose, tip rounded, base rounded to \pm tapering, outside often shallowly longitudinally ribbed, c. 1.5-2.3 \times 1.7-2.0 (-2.2) mm; pedicel (0.8-) 1-2 mm; perianth at anthesis cleft to c. 1/2-way, valves c. 0.2 mm thick. Androecium globose or depressed-globose, sometimes truncate-ellipsoid (see notes), 0.8-2.0 \times 0.8-1.3 mm, slightly laterally flattened or not and hence transverse section subcircular to ellipsoid; anthers 8-12 (-15), sessile, free apices 0-0.1 mm, towards apex curved over an apical cavity moderately broad to narrow, c. 0.2-0.4 (-0.5) mm deep; androphore rather narrow, c. 0.1-0.2 mm long; central column broad, solid. Female perianth ellipsoid, c. 2.5-3.0 \times 2.0 mm, glabrous, cleft at anthesis to c. 1/3,

valves 0.4 (-0.5) mm thick; ovary ovoid, glabrous, $1.5-1.7 \times 1.2-1.5$ mm, stigma minutely 2-lobed, c. 0.1 mm high; pedicel c. 1.0 mm long, glabrous, at base \pm articulated or not. Fruits 2-6 (-16, see notes) per infructescence, ellipsoid, top and base (narrowly) rounded, $2.2-3.4 \times 1.6-2.6$ cm, glabrous, drying glaucous-brown to dark brown, finely granulate, not tuberculate, dry pericarp 2-3 mm thick; stalk 2-3 mm long; perianth not persisting.

Distribution. India to Indo-China, and S. China, not in Malaya.

Note. This species, and the closely related *H. thorelii* and *H. longiflora* (see also there) have similar fruits. These three are akin to *H. glabra* from West Malesia, the latter distinctive by a number of minor characters, but always easily ascertained by the presence of blackish dots on the lower leaf surface. *H. subalpina* from mountainous West Malesia is also closely related.

KEY TO THE VARIETIES

- 1a. Leaf bud, upper portion of twigs, immature inflorescences and immature leaves with rusty woolly tomentum with hairs 0.5-1.0 mm long **b. var. lanata**
- b. Tomentum with greyish to dull brown hairs 0.1-0.2 mm long **a. var. amygdalina**

a. var. amygdalina

Leaf bud, young upper portions of twigs and immature inflorescences with tomentum of grey to dull brown hairs 0.1-0.2 mm long, or less. Mature Leaves usually membranous. Flowers in the same inflorescence either 2- or 3-valved or 2- and 3-valved mixed.

Distribution. India (Assam, Andaman Isl.), Bangladesh (E. Pakistan), Burma, S. China, N. Thailand, Laos, N. and C. Vietnam (Tonkin, N. and C. Annam).

INDIA (incl. E. Pakistan): *Hooker & Thomson* (coll. 11/50) *s.n.*; *Jenkins* (comm. Anderson) *s.n.*; *King's Coll.* 268; *Masters* (coll. *Simons*) *s.n.*; *Wallich* 6804, 6805 (belonging to the material of *M. exaltata*, not the lectotype); *de Silva & Gomes*, *Wall. Cat.* 6805.

Andaman Isl. (S. Andaman): *Balakrishnan* 1033; *Nair* 843, 3641; *King s.n.*, *Kings Coll. s.n.* (several dates).

BURMA: *Beddome s.n.*; *Dickason* 6556-bis, 6945; *Falconer* (comm. Anderson) 5446; *Helper* 4358; *Keenan*, *Tun Aung & Rule* 1569; *Kurz s.n.*, 984; *Wallich* 6797.

CHINA. Yunnan: *Huang Yun Wui* 120; also recorded S. Kwangsi, Hainan.

VIETNAM. Tonkin: *Bon* 2669, 4272, 4302; *Pételot* 1070; *Poilane* 13041; *W. T. Tsang* 29198 — C. & N. Annam: *Chevalier* 38164; *Poilane* 11106, 11119.

LAOS: *Poilane* 13700.

THAILAND. North: *Hansen*, *Seidenfaden*, *Smitinand* 11181, *Put* 796; *Winit* 1471.

Ecology: Evergreen forest, recorded from sandy soil; 0-1000 m alt. Flowers and fruits throughout the year.

NOTES

1. Flowers greenish-yellow or yellow, evil-smelling; fruits yellow.
2. Rather variable in shape and size of the inflorescence, and size of the male flower, including the androecium.

Wallich 6805 (de Silva & Gomes), from Sylhet (Bangladesh) rather deviates by its large, longish, male flower, the perianth measuring c. 2.2×2.2 mm, with the androecium exceedingly elongate, c. $1.8-2.0 \times 1.0$ mm; this specimen resembles *H. longiflora*, a species with the leaves apparently always distichous and with still larger flowers, to c. 3 mm long, and with the androecium with broader and longer tapering androphore, c. 0.3 mm long.

3. The specimens *Poilane 11106*, *11119* (from Annam), and *Poilane 13700* (Laos) seem to have a completely distichous phyllotaxis. Of these collections *Poilane 11119* somewhat deviates by its large infructescence bearing up to 16 (still immature) fruits; in most specimens only up to 6 fruits have been seen. In *Poilane 13700* the hairs on the leaf bud are relatively long for the variety, c. 0.2 mm.

4. Quite often the flowers in a specimen are in different stages of development; also fruits in the same infructescence are sometimes (e.g., *Balakrishnan 1033*) in different stages.

5. All specimens of both var. *amygdalina* and var. *lanata* were lumped by Sinclair in his large conception of *H. glabra*.

b. var. *lanata* de Wilde, var. nov.

Fig. 1A(5)

A var. amygdalina differt tomento lanuginoso rufo-ferrugineo in foliorum gemmis et inflorescentiis juvenilibus valde distincto, pilis 0.5 (-1.0) mm longis — Type: *Kerr 8556* (L; iso BM, K, P).

Leaf buds, immature twig apices, immature leaves (partly), and young inflorescences with dense conspicuous rusty woolly tomentum composed of hairs 0.5 (-1.0) mm long. Mature leaves chartaceous. Male perianths either 2-, or 3- or 4-valved. Female flowers and fruits not seen.

Distribution. E. Thailand, Cambodia.

THAILAND (E.): *Kerr 8439, 8556*.

CAMBODIA: *Pierre 1812, 5469*.

Ecology. Evergreen forest; 0-200 m. Flowers in February.

Vernacular name. Lûat-nok (E. Thailand).

Note. The specimens *Pierre 1812* (P), *5469* (BM) from Cambodia slightly differ from the plants from Thailand by the somewhat shorter tomentum with hairs c. 0.4-0.5 mm long, and by the predominantly 2-valved perianths.